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Chemical Features of the Subarctic Boundary Near 170°W[1]

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ABSTRACT

During the Yaloc 66 cruise of R/V *Yaquina*, the vertical distribution of nutrients, *p*H, alkalinity, apparent oxygen utilization, preformed phosphate, preformed nitrate, and specific alkalinity across the subarctic boundary near 170°W were studied. In addition to use of salinity to identify the subarctic boundary, the surface distributions of nutrients, *p*H, and preformed nutrients were found to be useful. Both the density-apparent oxygen utilization relationships and the specific alkalinity pattern indicated upward divergence of subsurface water having salinity greater than 34.0‰ on the north side of the boundary. A high specific alkalinity of about 0.129 immediately north of the boundary was probably due to the transport of upwardly diverged water having high specific alkalinity to near the boundary. Values for preformed phosphate and preformed nitrate gave supporting evidence that the origin of the salinity-minimum water located south of the boundary is in the subarctic region.

INTRODUCTION

One of the unique oceanographic features in the North Pacific Ocean is the subarctic boundary, approximately along 42°N. The boundary extends across the ocean from Asia to North America and is recognized by its anomalous isohaline structure. It is generally identified by a nearly vertical isohaline of 34.0‰ which extends from the surface to a depth of about 200 to 400 m (Dodimead et al., 1963).

North of the boundary, in the subarctic region, the salinity is lowest at the surface and increases with depth. South of the boundary, in the subtropic region, the salinity is highest at the surface and decreases to a distinct minimum below 500 m, but the water column is stable because of decreasing temperature (Dodimead et al., 1963).

The location of the boundary is important in high-sea salmon fishing, for the boundary is considered to be the southern limit of salmon (Dodimead et al., 1963). In view of the widespread interest in the subarctic boundary among fishery and oceanographic scientists, I have recently undertaken a chemical investigation of the boundary conditions from R/V *Yaquina* of Oregon State University.

OBSERVATIONS

R/V *Yaquina* crossed the subarctic boundary on June 17–18, 1966 during her voyage from Hawaii to Adak Island in the Aleutians. The cruise track and hydrographic stations are shown in Fig. 1.

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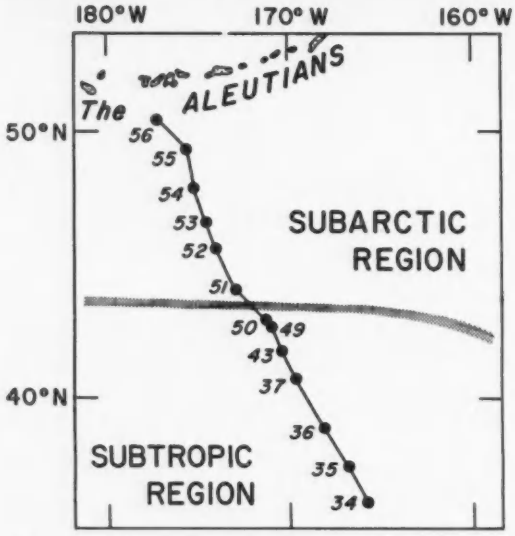

FIG. 1. Hydrographic stations across the subarctic boundary.

Although the water was sampled down close to the sea floor at most of the stations occupied, the hydrochemical data of the upper 1800 m are used to describe the chemical features of the boundary zone. Water samples were obtained from Teflon-coated Nansen bottles.

Water samples were analyzed at sea for salinity, dissolved oxygen, inorganic phosphate, *p*H, alkalinity, dissolved nitrogen, and total carbon dioxide. Samples obtained for nitrate and silicate determinations were frozen at sea and analysed ashore during October 26–November 8. The manual of Strickland and Parsons (1965) was used to determine dissolved oxygen, inorganic phosphate, *p*H, alkalinity, and silicate. Additional analytical techniques used are as follow.

Salinity – by an inductive salinometer manufactured by Industria Manufacturing Engineers Pty. Ltd., Sydney, Australia (Brown and Hamon, 1961).

Dissolved nitrogen and total carbon dioxide – by a gas chromatograph technique described by Park (1965).

Nitrate – by the method of Mullin and Riley (1955).

At the time of this writing, due to the uncertainty in the calibration gas used to determine the dissolved nitrogen and total carbon dioxide, the gas data are still under examination; therefore, they are not included here.

RESULTS

The salinity structure (Fig. 2) shows a sharp transition at the boundary between stations 50 and 51. As generalized by Dodimead et al. (1963, p. 38) a

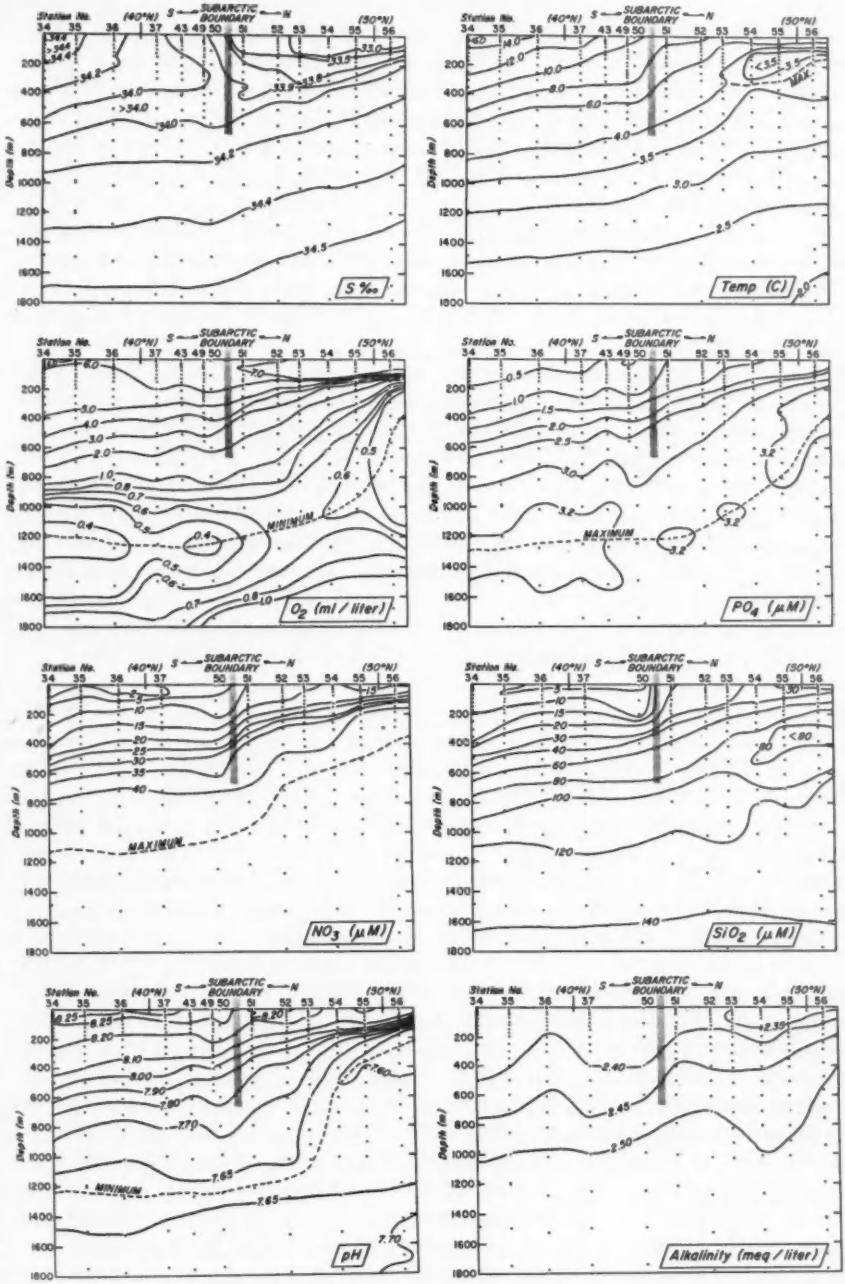

FIG. 2. Vertical distributions of salinity, temperature, dissolved oxygen, inorganic phosphate nitrate, silicate, *p*H, and alkalinity across the subarctic boundary.

nearly vertical isohaline of 34.0‰ extends from the surface to a depth of about 400 m. The salinity minimum, < 34.0‰, intrudes southward from the boundary at depths of 400 to 600 m. Below 600 m, the isohalines are horizontal on the south side of the boundary, but they gradually rise on the north side. Similar salinity structure is shown in Reid's monograph (1965, p. 51) along 160°W.

The temperature distribution (Fig. 2) shows a moderate ascent of isothermals across the boundary from south to north in the upper 400 m. Beneath 800 m, isothermal lines possess essentially the same features as the isohaline structure, i.e. they are horizontal on the south side and upward sloping on the north side of the boundary. A weak temperature maximum (3.5–3.9 C) was observable at the depth range of 140–300 m near the Aleutians (stations 53–56).

Oxygen, phosphate, nitrate, silicate, and *p*H (Fig. 2) show essentially the same isopleth patterns. Horizontal isopleths prevail on the south side of the boundary, and an upward trend of these isopleths starts at the boundary and continues toward the north. The oxygen minimum, phosphate maximum, nitrate maximum, and *p*H minimum are located at 1200 m in the subtropic region, and gradually rise in the subarctic region. Over the Aleutian trench, at station 56, these extremes exist at 200 to 400 m. Silicate isopleths show a very sharp gradient at the surface across the boundary, from approximately 5 μM in the subtropic to 20 μM in the subarctic region.

The alkalinity profile (Fig. 2) is relatively featureless. In general, one can observe a rise in its isopleths across the boundary and northward.

DISCUSSION

In addition to the use of the isohaline structure of 34.0‰ to locate the subarctic boundary (Dodimead et al., 1963), other chemical features are found to be useful. Across the boundary, from station 50 to 51, phosphate increases from 0.5 to 0.9, nitrate from 4 to 9, and silicate from 3 to 19 μM respectively. The surface *p*H's drop from 8.27 to 8.18. The sharpest change in chemical features across the boundary is in silicate concentration.

The salinity and temperature data in Fig. 2 indicate that a temperature–salinity (T–S) diagram can clearly distinguish the two adjoining water masses at the boundary. Figure 3 shows the distinct separation. The subtropic water shows essentially the same features the Eastern Pacific water possesses (*see* Dodimead et al., 1963, p. 37); the only difference is that the salinity of the subtropic water is about 0.6‰ less than that of the Eastern Pacific water at a given temperature. The T–S patterns of the northern stations are similar to the subarctic T–S diagram given by Dodimead et al. (1963). Below 800 m all the stations examined had identical T–S patterns, although the depth of a given T–S point from one station to another differed by as much as 500 m. According to Fig. 3, we can still distinguish the two water masses at a salinity of 34.1‰. The depths of 34.1‰ are about 700 m in the subtropic region and range from 300 to 600 m in the subarctic region.

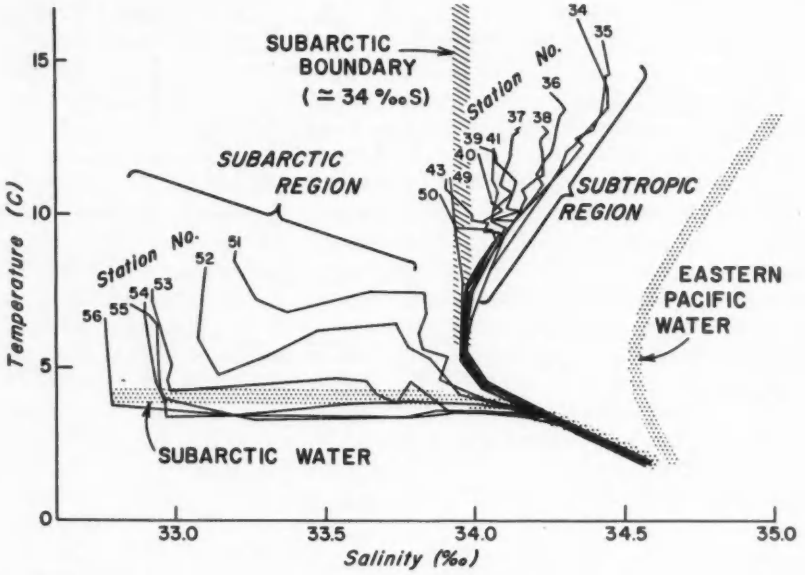

FIG. 3. Composite temperature–salinity (T–S) distribution across the subarctic boundary. The T–S patterns (dotted bands) for both subtropic and subarctic waters are from Dodimead et al. (1963, p. 37).

The correspondence of the oxygen, phosphate, nitrate, and *p*H distributions in Fig. 2 is not surprising, for these chemical entities are strongly related to the production and consumption of organic matter in the ocean. When organic matter is oxidized, inorganic phosphate, inorganic nitrogen nutrients, and carbon dioxide are released. The final oxidation product of the inorganic nitrogen nutrients (ammonia, nitrite, and nitrate) is nitrate. The increase in carbon dioxide lowers the *p*H of seawater. Therefore, from a biochemical point of view, the oxygen minimum should be closely related to both the phosphate and nitrate maxima and the *p*H minimum. Indeed, the cruise data agree well with the biochemical oxidation mechanism.

Although silicate is a plant nutrient, for diatoms mainly, its dissolution mechanism is complicated by inorganic dissolution. Consequently, the vertical profile of silicate shows an ever increasing trend with depth, and it does not show a maximum at near the oxygen minimum zone.

To further examine chemical conditions across the boundary, density (σ_t), apparent oxygen utilization (AOU), preformed phosphate and nitrate, and specific alkalinity are plotted in Fig. 4. The vertical σ_t distribution shows that the waters on both sides of the boundary are stable with respect to depth as previously stated by Dodimead et al. (1963).

AOU was calculated by subtracting the measured oxygen value from the 100% oxygen saturation value of Green (1965). The oxygen saturation

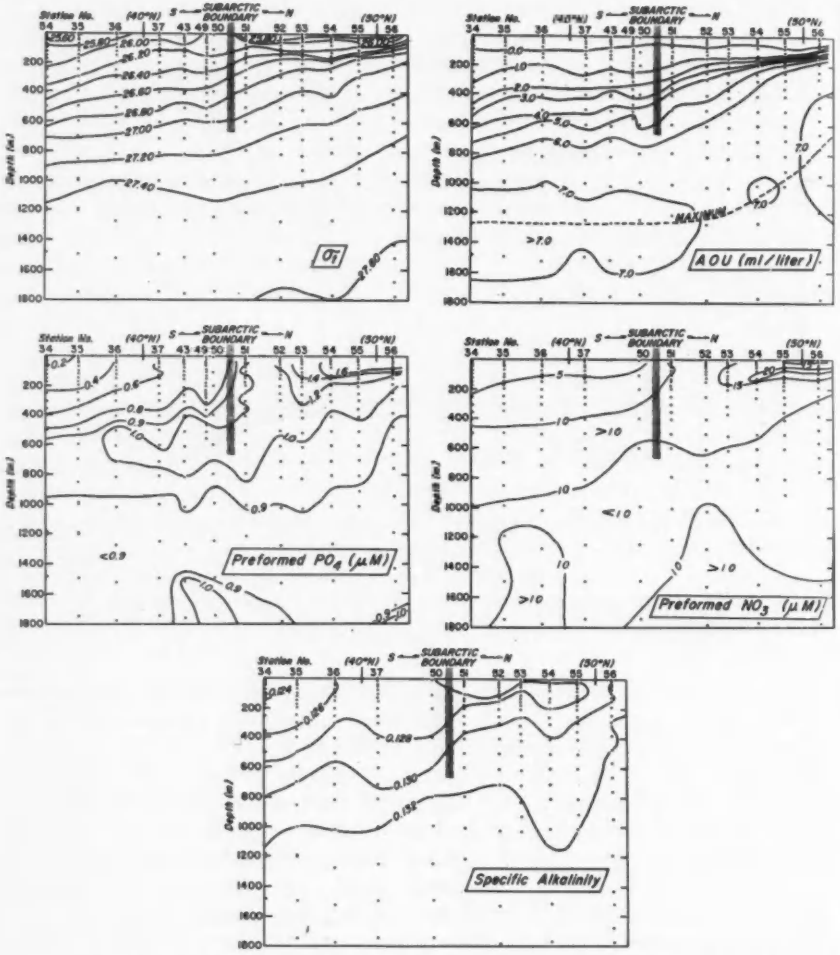

FIG. 4. Vertical distributions of σt, AOU, preformed phosphate, preformed nitrate, and specific alkalinity across the subarctic boundary.

values were previously corrected for the atmospheric vapor pressure. Figure 4 shows a negative AOU of about 0.3 ml/liter within the upper 100 m. The negative AOU can be formed either by primary production or by warming up of the surface water. Since the water samples were taken in the mid-June, both the spring phytoplankton bloom and an increase in surface temperature can produce the negative AOU. The depth of the AOU maximum was very near the depth of the oxygen minimum.

σ_t–AOU Relationship

The σ_t–AOU relationship was used to study the direction of water flow at intermediate depth (1000~2000 m) in the Northeastern Pacific Ocean by Pytkowicz and Kester (1966). Similar treatment for my cross section (Fig. 5) shows that AOU is constant along the southern half of the cross section. However, in the northern half, in the subarctic region, it increases northward along the σ_t surfaces of 26.80, 27.00, 27.20, and 27.40. If we assume that the water movement along these σ_t surfaces is along a north–south axis, then the increasing AOU to the north suggests that the northern water is older than the southern. We can, therefore, tentatively conclude that the water is moving from south to north. Since these σ_t surfaces are ascending as one goes north, the water appears to be diverging upward. Since no high-salinity water is forming in the subarctic region, the highly saline water of 34.2–34.5‰ found at comparatively shallow depth (400~1200 m) near the Aleutians must come from the subtropic region (900–1700 m) and must be upwelled in the subarctic region. Examination of the σ_t–AOU relationship supports the existence of the above mechanism. A similar suggestion that water of salinity greater than 34.0‰ upwells into the subarctic region was made by Dodimead et al. (1963, p. 16).

Preformed Phosphate and Preformed Nitrate

Preformed nutrients are conservative properties of a given water mass (Redfield et al., 1963, p. 33). They are defined as the amount of inorganic nutrients that existed in the water before it sank from the surface layer. Oxidation of organic matter *in situ* changes total inorganic nutrients but not preformed nutrient concentrations.

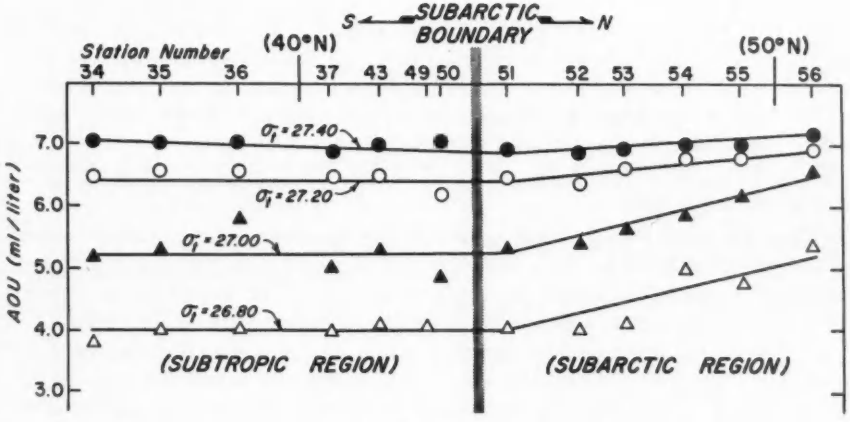

Fig. 5. AOU along the σ_t surfaces of 26.80, 27.00, 27.20, and 27.40.

In general, preformed phosphate can be calculated by the following formula.

$$\text{Preformed phosphate} = (\text{measured phosphate}) - \frac{\text{AOU (ml/liter)}}{3} \quad \ldots\ldots(1)$$

The phosphate concentration is expressed in μM unit, which is equivalent to μg-at/liter.

Near the surface the preformed phosphate concentration (Fig. 4) increases across the boundary from 0.2 (station 34) to 1.7 μM (station 56). Between 1000 and 1400 m it is in a narrow range of 0.8–.09 μM. Near the boundary, the 1.0-μM preformed phosphate isopleth is almost vertical from near the surface to 400 m. The isopleth then turns southward along the salinity minimum zone to over 200 miles south of the boundary. Since the preformed phosphate is a conservative property within a water mass, the salinity minimum water in the subtropic region, having a preformed phosphate concentration of over 1.0 μM, belongs to the same water mass as that existing immediately north of the boundary. This evidence supports the premise that the low-salinity water, <34.0‰, intruded southward originates from the subarctic water.

Preformed nitrate may be calculated in the same manner as shown in equation 1 using the oxidation change in N : P ratio of 16:1 cited by Redfield et al. (1963). Its equation is as follows.

$$\text{Preformed nitrate} = (\text{measured nitrate}) - \frac{16\ \text{AOU (ml/liter)}}{3} \quad \ldots\ldots(2)$$

A caution has to be taken to consider the effect of *in situ* oxidation of nitrite and ammonia into nitrate, which changes the AOU:N ratio. Since it is not possible to ascertain the magnitude of both nitrite and ammonia before the water sank from the surface, I assume that equation 2 is applicable to estimate preformed nitrate only in the first approximation. Figure 4 shows the vertical distribution of preformed nitrate calculated on the above assumption. The overall trend of the preformed nitrate isopleths is similar to that of preformed phosphate. It, too, indicates that the salinity minimum water in the subtropic region originates in the subarctic region.

Specific Alkalinity

Specific alkalinity does not vary with addition or removal of fresh water or carbon dioxide to or from seawater. It changes with calcium carbonate precipitation and dissolution occurring in seawater. The usefulness of specific alkalinity in tracing a water mass is explained below with an example.

Suppose we have freshly upwelled water that has an alkalinity of 2.47 meq/liter and chlorinity of 19.0‰. Its specific alkalinity is 2.47/19.0, or 0.130. At the surface, suppose the water has moved to a new location, and on the way its chlorinity is lowered by rain to 18.0‰. The resulting alkalinity should

decrease proportionally to 2.34 meq/liter. Yet the specific alkalinity of the diluted water remains at the original value of 0.130. This fact is useful in tracing backward to the original upwelled water.

In the subtropic region the surface specific alkalinity (Fig. 4) is lower than 0.128. In general, the isopleths of specific alkalinity ascend as we go north across the subarctic boundary.

The 0.130 isopleth of specific alkalinity exists at 600–800 m in the subtropic region, and it intersects the sea surface at the Aleutian Trench (station 56). Similarly, the 0.132 isopleth is near 1000 m in the subtropic region, but its depth over the Aleutian Trench is only about 300 m. These observations, along with the σ_t–AOU relationship, give supporting evidence of the upward divergence of saline water having a salinity over 34.0‰ near the Aleutian Trench in the subarctic region.

In the surface layer immediately north of the boundary, we find a lens-shaped body of water having a high specific alkalinity of 0.129 (Fig. 4). A probable explanation for this is that upwelled water having a high specific alkalinity of about 0.129 was transported to the area near the boundary zone. Detailed combined studies of the specific alkalinity and surface water movement in the subarctic region will elucidate its origin.

ACKNOWLEDGMENTS

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A Continuous Size Spectrum for Particulate Matter in the Sea[1]

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ABSTRACT

The size spectrum of particulate material in seawater can easily be expressed as total particle volume versus the logarithm of particle diameter. This appears to be the most informative way to present the data and it is also aptly suited to the classical divisions of nanno-, micro-, and macroplankton.

A realistic measure of the volume of irregularly shaped particles such as phytoplankton chains could be made with a Coulter Counter. Particle volume measurements were in good agreement with estimates based on microscopic determination of particle diameter. There were also highly significant correlations between total particle volume, as indicated by the counter, and particulate carbon and nitrogen.

INTRODUCTION

Methods which have been generally employed to estimate the quantity and size distribution of particulate material suspended in seawater include filtration using filters of different pore size (Mullin, 1965), counting and sizing with a microscope (Riley, 1963), and measurement of light transmission and scattering (Jerlov, 1961). The technical operation of the Coulter Counter[2] for measuring the size distribution of particulate matter in the sea has also been described (Sheldon and Parsons, MS, 1966). The latter technique appears to have two distinct advantages in that it is more rapid and gives more detailed results than any previous method. In this report results are presented from field observations which clearly demonstrate that the Coulter Counter can be of considerable value for determining the particle content of seawater.

METHODS

In the following discussion the results of counts made with the Coulter Counter are given in terms of particle diameter. However, as the instrument actually measures particle volume it should be understood that the particle diameter given refers to that of a sphere with the same volume as the particle.

The data presented in this paper were obtained as part of a 2-month time-series study carried out in Saanich Inlet, British Columbia, during June and July 1966. Seawater samples were analysed immediately after collection

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[2]A patented instrument manufactured by Coulter Electronics, 590 West 20th St., Hialeah, Florida.

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for particle size distributions and for total particulate carbon and nitrogen. The samples for particulate carbon and nitrogen analyses were collected by filtration onto glass fibre filters (Whatman GFC), and the carbon and nitrogen contents were determined by total combustion using Coleman carbon and nitrogen analysers.

OBSERVATIONS AND DISCUSSION

A characteristic feature of suspended particulate matter in seawater is that particles of widely different sizes are present. In order to extract the maximum amount of information from a given set of data it is necessary to carefully select the correct grade scale for particle size distributions. The easiest application of the Coulter Counter is to count particles within selected limits of particle volume. This is convenient for certain types of closely graded particle distributions, and has been used in studies on blood and various other kinds of cells. In marine work particle volume has been used in studies of both unicellular (El-Sayed and Lee, 1963; Hastings et al., 1962) and multicellular (Parsons, 1965) planktonic organisms. However, for measurements of particulate matter in the sea the most informative arrangement of data is obtained when particle counts are expressed as volume (or biomass) on a logarithmic scale of particle diameter.

This is illustrated in Fig. 1 where three curves have been plotted using the same data from a sample of seawater in which a bloom of *Skeletonema costatum* occurred. In Fig. 1A the data are shown as they would be most easily read from the counter (i.e. numbers of particles in selected ranges of particle volume). Except for the smallest particle volume setting, the counts in each grade were too small to show clearly on the graph. Figure 1B gives numbers of particles in selected ranges of particle diameter. Although this figure was compiled from data obtained with the Coulter Counter, particle counts made with a microscope would be most easily expressed in the same way. In Fig. 1C, the concentration of particles on a logarithmic scale of particle diameter is given. It is only in this curve that the presence of a diatom bloom becomes apparent. Presentation of data in the form shown in Fig. 1C rather than that shown in Fig. 1A is not difficult if the counts are made on a previously defined logarithmic scale such as the one suggested by Sheldon and Parsons (MS, 1966).

In Fig. 2, examples are given of distributions of suspended matter at two depths. The curves giving number of particles indicate only that fewer small particles were present at depth, but the curves giving concentration show that the total biomass was less over the whole size range at the greater depth. It is further possible to identify exactly where in the size spectrum the greatest decrease in biomass occurred by noting the presence of two peaks in Fig. 2B and the marked absence of the first peak in Fig. 2D.

Figure 3 shows the continuous size distribution of particulate material, with diameters from 3 to 1000 μ, which occurred during June in Saanich Inlet. In order to obtain this size spectrum it was necessary to employ three aperture

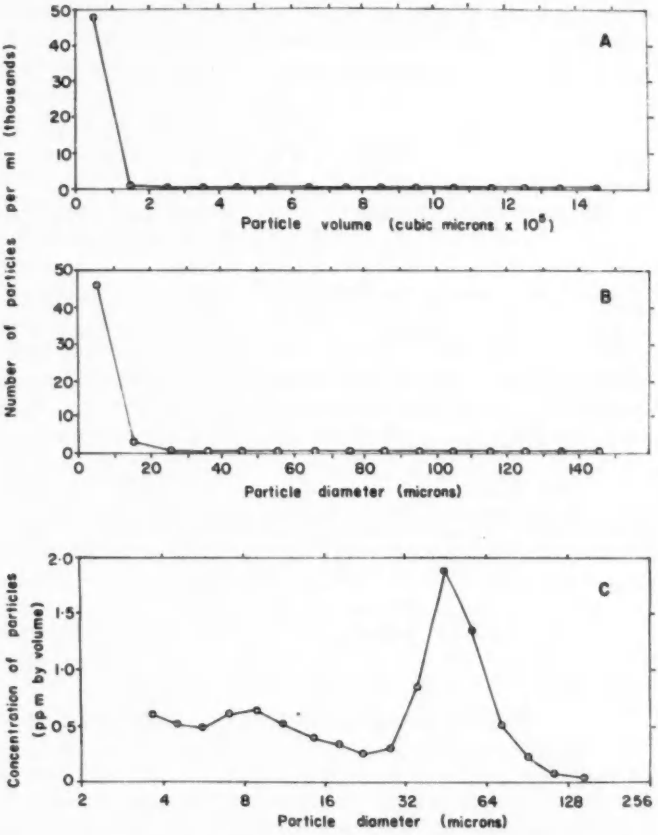

FIG. 1. Particulate matter in a single sample of seawater taken during a bloom of the diatom *Skeletonema costatum*. A, numbers of particles versus particle volume; B, numbers of particles versus particle diameter; C, concentration of particles versus particle diameter on a logarithmic scale.

sizes on the Coulter Counter. The larger particles (with diameters greater than 300 μ) were filtered onto 300-μ netting and then resuspended in membrane-filtered seawater at a suitable concentration. After measuring the size distribution of particles, the results were recalculated to give concentration of large particles in the original sample. In this particular distribution the traditional classification of nannoplankton, microplankton, and macroplankton is shown, following the definitions of Dussart (1965, corrected for a typographical error in the original; Dussart 1966, personal communication). By combining the logarithmic scale suggested here with the plankton divisions given by Dussart (1965), the latter divisions are given equal space on the logarithmic

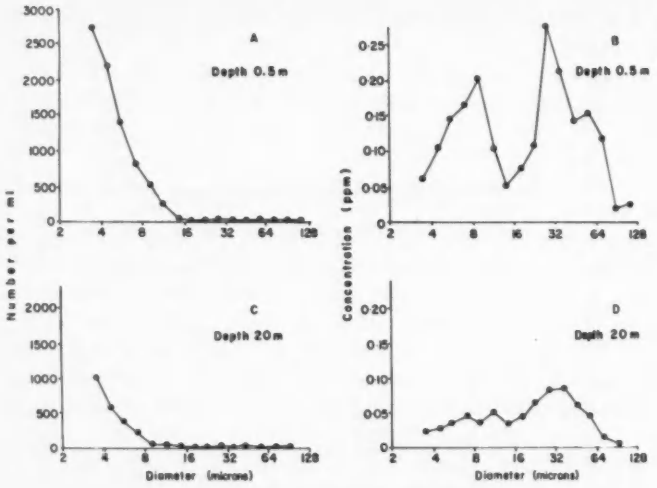

FIG. 2. Particulate matter in two samples of seawater taken at two depths. A and C, numbers of particles versus particle diameter on a logarithmic scale; B and D, concentration of particles versus particle diameter on a logarithmic scale.

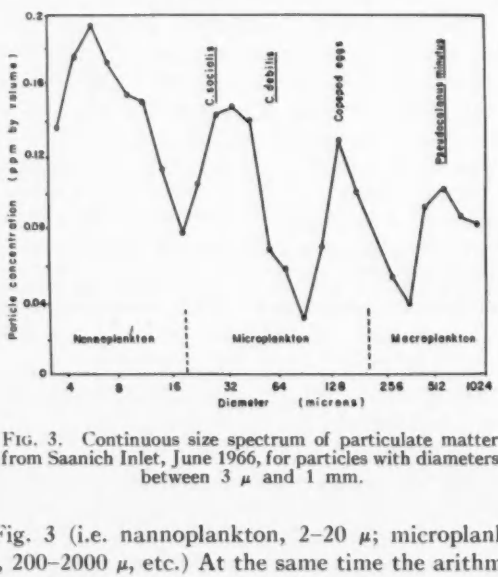

FIG. 3. Continuous size spectrum of particulate matter from Saanich Inlet, June 1966, for particles with diameters between 3 μ and 1 mm.

scale used in Fig. 3 (i.e. nannoplankton, 2–20 μ; microplankton, 20–200 μ; macroplankton, 200–2000 μ, etc.) At the same time the arithmetic progression of cell volumes on which this scale is based is ideally suited to electronic sizing.

The greatest biomass in Fig. 3 occurs among the nannoplankton (unidentified), and a mixture of the diatom species *Chaetoceros socialis* and *C.*

debilis makes up a sizeable fraction of the boimass of the microplankton. The size distribution of copepod eggs extends from micro- to macroplankton, and a portion of the macroplankton is represented by the copepod *Pseudocalanus minutus* which forms a peak at a diameter of about 600 μ. The dimensions of *P. minutus* were approximately 1.0 by 0.4 mm along its major and minor axes which gives a volume of 0.084 mm^3 if the animal's shape is assumed to approximate that of a prolate spheroid. It is of interest to note that the peak of the size distribution for this animal is only slightly more than the radius of a sphere having a volume of 0.084 mm^3.

The difficulty of deciding exactly what the counter records in terms of biomass has been one of the more controversial points to resolve when working with this type of instrument (e.g. see discussion by Hastings et al., 1962), but for most practical purposes the response of the instrument to irregularly shaped particles appears to be essentially proportional to particle volume. For example, in Fig. 3 the peak occurring between particle diameters of 20 and 80 μ represents a mixed population of the two chain-forming diatom species *Chaetoceros socialis* and *C. debilis*. Measurements made with a microscope showed that *C. socialis* cells were approximately 10 μ in diameter with about 30 cells in an average chain, and *C. deblis* cells had a diameter of approximately 20 μ with 20 cells per chain. If, as a first approximation, we assume that each individual cell was spherical, then an average *C. socialis* chain would have a total volume of about 16,000 μ^3, and a *C. debilis* chain would be about 84,000 μ^3. These would be shown on Fig. 3 as particles with diameters of about 31 and 54 μ. These results are not unreasonable. From this approximation it appears that a realistic measure of absolute biomass can be obtained with the instrument, even when dealing with irregularly shaped particles.

More direct evidence of the above point is to be found in Fig. 4 and 5. In these more than 70 measurements of total particle concentration measured by the Coulter Counter (i.e. found by adding together the concentrations for each grade) have been correlated against determinations of particulate carbon and nitrogen. The correlation coefficients for particle concentration against particulate carbon (0.88) and particle concentration against particulate nitrogen (0.52) are both significant ($P < .01$). If a density of unity is assumed for the particulate material and a factor of 0.1 is used to convert wet to dry weight, then the equations (determined as the reduced major axes; Kermack and Haldane, 1950; Imbrie, 1956) give a carbon to dry weight ratio of 0.52 and a nitrogen to dry weight ratio of 0.093. These values are within the upper limits for pure cultures of phytoplankton (Parsons et al., 1961), but are probably high for natural populations. This might reflect an underestimation of absolute volume as measured by the Coulter Counter, or it could indicate that there were significant amounts of inorganic material in suspension, the density of which would be greater than unity. It should also be considered that the amounts of carbon and nitrogen in organic matter are variable, and although a high degree of correlation between these constituents and the total volume of organic matter might be expected, the relationships shown in Fig. 4 and 5

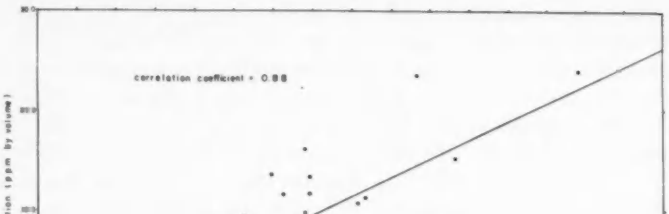

FIG. 4. Relationship between concentration of particulate matter as measured by the Coulter Counter and particulate carbon measured chemically. Particle concentration by volume = 19 (carbon concentration by weight) — 3.56.

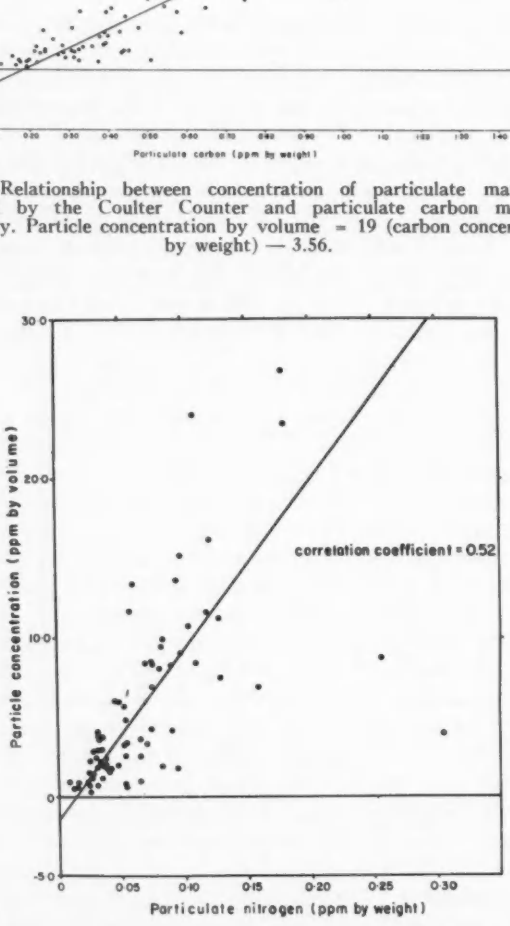

FIG. 5. Relationship between concentration of particulate matter as measured by the Coulter Counter and particulate nitrogen measured chemically. Particle concentration by volume = 107 (nitrogen concentration by weight) — 1.4.

are probably a characteristic of the particular environment studied. Furthermore, it should be emphasised that the relationships in Fig. 4 and 5 are probably linear over the range shown. But if a greater range had been considered the relationships would have been logarithmic because larger organic particles contain relatively smaller proportions of carbon and nitrogen (Mullin et al., 1966).

Other features of interest in Fig. 4 and 5 are the intercepts on the axes for particulate carbon and nitrogen. These were obtained simply by extrapolating each line beyond the range of observations to apparently negative values of particle concentration. The fact that carbon and nitrogen were present in particles which were not detected by the counter is not surprising. The filters used in the determinations of particulate carbon and nitrogen retained all particles with diameters greater than 2 μ, but the data on total volume measured by the counter were only for particles with diameters between 3 and 200 μ, as this was the range within which most of the phytoplankton occurred and over which counts were routinely made. Thus the intercepts on the graphs are a measure of the particulate material not estimated by the Coulter Counter.

ACKNOWLEDGMENTS

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Fecundity of Steelhead Trout, *Salmo gairdneri*, from Alsea River, Oregon[1]

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ABSTRACT

In a sample of 73 females of winter steelhead, *Salmo gairdneri* Richardson, from the 1965–66 spawning run in the Alsea River, Oregon, egg size and egg number were correlated with body length. Alsea steelhead produced approximately 32% fewer eggs than females from Trinity River, California, and 51% less than fish of similar size from Scott Creek, California.

INTRODUCTION

Little attention has been directed toward fecundity of steelhead trout, *Salmo gairdneri* Richardson, even though the variable is of much importance in the population dynamics of anadromous salmonids. As part of a continuing investigation by the Oregon Game Commission into the life history of steelhead from Alsea River, Oregon, data on fecundity of winter steelhead were collected from the 1965–66 spawning run. Fecundity as used in this paper is defined as the number of eggs brought to maturity by a single female.

METHODS

Data for the present study were collected at the peak of the spawning run from 73 steelhead entering the upstream trap located on the North Fork of the Alsea River about 40 miles above the ocean. The sample consisted of 28 green and 45 ripe females.

Fish selected for study were anesthetized with chloretone, measured to the nearest millimeter in fork length and weighed to the nearest gram. Fecundity was determined in two ways. Green fish used for gonadal measurements were killed; the gonads were removed, weighed, and then preserved prior to manual counting of the eggs. Eggs from ripe fish were measured volumetrically by the Taft method (Shapovalov and Taft, 1954) immediately after being stripped from the fish. The method allows the estimation of egg production without loss of fish or eggs. Total egg volume was measured in a 1000-cc graduate; lots of 10 eggs were measured by water displacement in a 10-cc graduate. Multiplication by a volume correction factor of 0.840 reduced the measured volume to actual volume of eggs. Eggs from 13 fish were measured volumetrically and then counted to calculate the volume factor. The number of

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eggs was then calculated by dividing corrected egg volume by the mean volume of a single egg from that fish.

The number of eggs from ripe fish determined volumetrically was adjusted by an egg retention factor of 18.2% based on examination of 21 females. Fish used for estimating retention were first hand-stripped by an experienced hatcheryman and then killed. Mature eggs retained in the body cavity were extracted and counted. Range in retention was 8.8–35.8%.

A sample of 28 green fish was used to check the possibility of egg loss from ripe females prior to capture. Eggs of the fish selected were of full size but still enclosed in the ovarian membrane. Atretic eggs were not included in the count. Further atresia was considered to be negligible as the eggs were of similar size to eggs from ripe females. The 28 green fish had a similar fecundity–body length relationship to the 45 ripe females used in the study ($F = 3.6$; tabular $F = 8.6$; $P = 0.05$). Thus, if any eggs were lost from the ripe females prior to capture, the quantities were not sufficient to alter seriously the fecundity figures for Alsea steelhead presented in this paper.

RESULTS

Egg Size

A positive correlation exists between egg size and body size in most salmonids (Rounsefell, 1957) and a similar relationship was apparent in Alsea steelhead. Mean volume of eggs from 37 three-year-old females (1/2)[3] ready to spawn was 0.108 cc with a range of 0.090–0.125. Eight 4-year-old fish (1/2S.3) had eggs ranging in size from 0.120 to 0.170 cc with a mean of 0.148. Eighty per cent ($r = 0.89$) of the variation in egg size in a sample of 45 Alsea fish of the two age-groups was associated with body length. Scott (1962) felt that some factor other than size of fish or diet predetermined egg size of non-migratory rainbow of the same age although he did find that 4-year-old second spawners from Pennask Lake produced larger eggs than the 3-year-old fish. Nikolskii (1962) maintains that egg size is related to nutrition. In our sample of Alsea steelhead, egg size was highly correlated ($r = 0.99$) with body size for initial spawners of the same age (1/2) and strongly correlated as mentioned above when 3- and 4-year-old fish were combined. The relation of egg size to body size (Fig. 1) is described by the formula:

$$Y = -0.0734 + 0.00029\ L$$

where Y = egg volume in cubic centimeters and L is the body length in millimeters.

These data point up the possible disproportionate contribution of a few large older spawners to the resulting year-class as reported by Foerster and

[3]Terminology follows Maher and Larkin (1954). Numerals on the left of the oblique indicate years of freshwater growth; on the right, years of saltwater growth. A fish designated as 2/2S.3 would have completed 2 years of freshwater growth, would have spawned after 2 years of ocean life, and would be approaching the end of 3 years of marine growth.

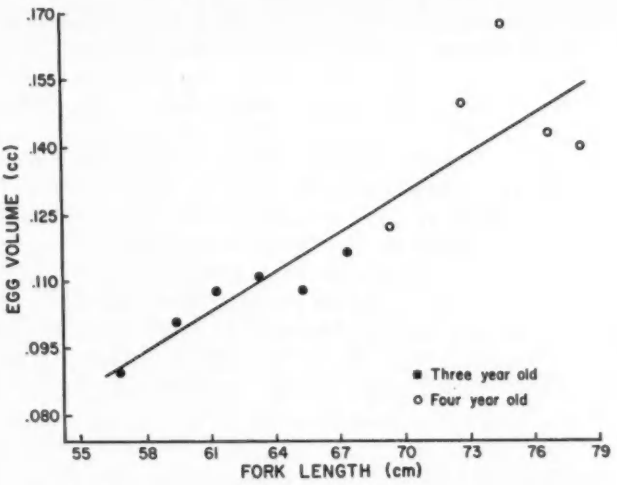

FIG. 1. Relation of egg size to fork length of 45 Alsea River steelhead trout collected from the 1965–66 spawning run.

Pritchard (1941). The reasoning behind this statement is that older fish not only produce more eggs because of their larger size but also produce larger eggs. Fry resulting from large eggs would have better chance of survival than fry hatched from small eggs (Svardson, 1949; Privolnev, 1960). Further investigation is needed on Alsea steelhead to determine if survival is higher among fry produced from large eggs, but caution should be used in killing initially spawning steelhead in any hatchery egg-taking operation. Steelhead which return to spawn naturally the second time might produce a large portion of the wild fish in the population.

Within the sample of 73 fish, 14 were unmarked and determined to be of wild origin. Most of each spawning run on the North Fork has been used for egg-taking purposes during the last several decades. The balance of the run spawn naturally. Large numbers of the hatchery-reared smolts are released into the stream each year. Thus, wild steelhead on the North Fork of the Alsea River are common stock with hatchery fish released among them, and any comparison between wild and hatchery fish would essentially be testing differences in the freshwater life of the fish (i.e. hatchery-rearing versus stream-rearing). In "*t*"-tests for common slope and origin, the fecundity–length relationship of wild and hatchery fish could be expressed by a single regression line ($P = 0.05$). Although sample sizes were small, it does appear that ocean growing conditions are more important in determining egg production in the Alsea steelhead than freshwater conditions prior to seaward migration.

FECUNDITY IN RELATION TO BODY AND EGG SIZE

Shapovalov and Taft (1954) found a curvilinear relationship between fecundity and body length of Scott Creek steelhead. A straight line adequately

described the relationship between body length and egg numbers in the sample of 73 Alsea steelhead (Fig. 2). The relationship is expressed by the formula:

$$E = -5054 + 130.53\ L$$

where E = number of eggs produced and L = fork length in centimeters. Hence, fecundity increased by about 131 eggs for each increase in body length of 1 cm within the range of 55–77 cm. The 73 fish in the sample had a mean length of 64.9 cm and produced an average of 3438 eggs each.

The correlation of fecundity on body length ($r = 0.77$) indicated that approximately 59% of the variation in egg production was associated with body length. The relation of fecundity to body weight ($r = 0.81$) was slightly closer than for length as 65% of the variation in fecundity was associated with weight. The relation of body weight to egg production is expressed by the formula:

$$E = 747 + 0.967\ W$$

where E = number of eggs produced and W = body weight in grams.

It was somewhat surprising that egg number agreed more closely with body weight than length. Steelhead lose condition from the time they cease active feeding on approaching fresh water, as do salmon, but body length should remain unchanged (Pope et al., 1961). Consideration of length and weight together with fecundity accounted for little additional variation in egg numbers. Only 75% of the variation in fecundity (R = 0.86) was associated with combined length and weight, partially because of the strong interaction between the two variables ($r = 0.95$).

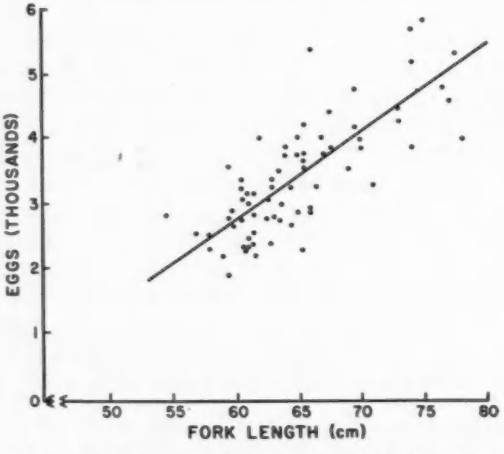

FIG. 2. Fecundity–length relationship of 73 Alsea River steelhead trout collected from the 1965–66 spawning run.

Egg size and body length were compared with fecundity to determine if differences in egg size could account for the variation in fecundity not attributable to fish size. If egg size is influenced by nutrition as maintained by Nikolskii (1962), then it is possible that a fish producing fewer eggs could produce larger eggs within limits than if it were producing numerous eggs. A positive correlation was found between egg size and fecundity ($r = 0.88$, $P = 0.05$) in a sample of 44 Alsea steelhead. Comparison of egg size and body length with fecundity ($r = 0.89$) accounted for slightly more variation in fecundity than when egg size or body length was considered alone.

McFadden et al. (1965) state that the use of ovary weight as a measure of fecundity in contrast to egg number is desirable because weight overcomes the influence of differences in egg size. In a sense, ovary size provides an estimate of the ability of the female to mobilize material for reproduction. The correlation of gonad weight with body length of 28 steelhead used previously for measuring egg loss was 0.80 and accounted for 11% more variation in fecundity than when the numbers of eggs from the same fish were compared with length ($r = 0.73$). Gonad weight appears to vary less in relation to body size than egg number from this comparison, but frequently it is undesirable to kill the female in order to weigh the gonads. The number of mature eggs provides a satisfactory measure of steelhead fecundity, and the female need not be killed when the method is used.

Alsea Versus Other Streams

Few studies have been made of variations in steelhead fecundity among different stocks. Data from Meigs and Pautzke (1941) indicated an average egg take of 3128 eggs per female from Green River, Washington, during 1939, 1940, and 1941. As mean body length and egg retention were not reported, the fecundity estimate could not be compared with data from other populations. Data on steelhead fecundity from Scott Creek, California (Shapovalov and Taft, 1954), and more recent unpublished data from Big Creek, Oregon, and Trinity River, California, were suitable for comparison with Alsea stock.

Data were obtained on 30 steelhead taken from the 1965 and 1966 spawning runs in Big Creek, Oregon,[4] to compare Alsea fish with steelhead from another Oregon stream. Big Creek is a small stream less than 15 miles in length that enters the Columbia River near its mouth approximately 120 miles north of the Alsea River. Eggs from the Big Creek fish were manually counted in the manner described for Alsea steelhead. Big Creek data from 1965 and 1966 were combined because the relationship of fecundity to body length of fish in the two samples could not be separated by tests for differences in slope and origin of the regression lines. Regression of egg production on length of Big Creek steelhead is described by the formula:

$$E = -2078 + 90.802\,L$$

[4]Data courtesy of Ernest R. Jeffries, Director of Fish Culture, and Vernon P. Knowles, Superintendent, Big Creek Hatchery, Oregon Fish Commission.

where E = number of eggs produced, and L = fork length in centimeters.

In comparing samples from the two streams it was not possible to reject the hypothesis that Big Creek and Alsea steelhead have similar fecundity (P = 0.05). However, fecundity of the Alsea sample could not be described by the fecundity–length formula computed from Big Creek data as far as origin of the regression line was concerned. Results of the *t*-tests were as follows:

Comparison	Degrees of freedom	*t* value	Tabular *t* (P = 0.05)
Common slope	99	1.73	1.98
Common origin			
Big Creek on Alsea	28	1.88	2.05
Alsea on Big Creek	71	3.54	1.99

Geographical and annual variations in salmonid fecundity as well as individual variations among the fish of the same size have been reported in other parts of the world. Fecundity differences have even been reported within a single spawning run as the season progresses but such are probably due to variations in atresia, age, or body size. Even in view of the different environmental causes of variation in fecundity within a species, the large differences between steelhead from Alsea River, and Trinity River and Scott Creek, California, were surprising. The Trinity River is located in northern California approximately 200 airline miles south of the Alsea River and 210 miles north of Scott Creek. In 1965, fecundity data were collected from 14 steelhead trapped in the Trinity River.[5] Fish in the sample ranged in length from 21.0 to 24.5 inches with a mean length of 22.5 inches (57.1 cm) and produced an average of 3540 eggs each by actual count. An Alsea fish measuring 22.5 inches would produce approximately 2424 eggs. According to the fecundity formula given by Shapovalov and Taft (1954), an average Scott Creek female 22.5 inches long produces 4964 eggs.

A trend of increasing fecundity toward the southern part of the range of the species appears when data from the streams mentioned above are compared (Fig. 3). Fish from Big Creek do not fit the trend but this may be due to sample size since the Big Creek sample was not statistically different from the Alsea sample. Rounsefell (1957) reported a similar trend of increasing fecundity southward in the genus *Oncorhynchus* and suggested increased growth rate as a possible causal factor worth exploring. The basis of his suggestion was that the average age at maturity of most species of salmon tends to increase toward the north, and Karluk Lake sockeye maturing after 2 years at sea had a higher fecundity than sockeye of the same length spending 3 years at sea. That is, fish maturing at a young age may produce more eggs than slower-growing fish which reach maturity later. Rounsefell found an inverse

[5]Data courtesy Donald H. Fry Jr., California Department of Fish and Game.

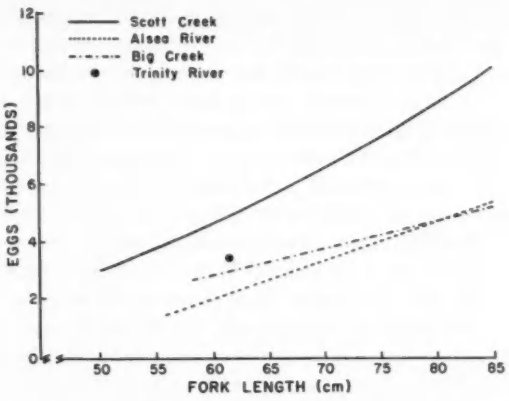

FIG. 3. Fecundity of winter steelhead trout from four California and Oregon streams.

relationship between fecundity of pink salmon from Queen Charlotte Island and mean monthly summer sea temperature. In years of cool summer ocean temperatures, fecundity was lower because of slower growth. The relationship could also hold true for the steelhead as ocean temperatures tend to be warmer toward the southern portion of its geographic range (Withler, 1966). Withler reported that steelhead are similar to salmon in that the average age at maturity for steelhead increases northward. Steelhead in the northern portion of their range spend a longer time in fresh water prior to downstream migration on the average and also longer at sea before reaching maturity as the result of slower growth.

Low water temperature affects fish growth by depressing the metabolic rate and reducing food conversion. A similar effect on growth results from inadequate food supply. Scott (1962) found that the amount of food available during maturation regulated fecundity of rainbow trout. Starved (and presumably slower-growing) fish had higher follicular atresia than did fish supplied with adequate food, resulting in a lower number of eggs being brought to maturity. McFadden et al. (1965) found that growth and fecundity of brown trout were directly related to the fertility of the stream environment. Regardless of whether temperature alone or temperature and food supply produced the north–south gradient in fecundity of steelhead noted above, a similar gradient should be apparent in body size at maturity. Scott (1962) stated that diet restrictions imposed in his study appeared to have little or no lasting effect on physical condition of the fish. One might conclude from his statement that the effect of low temperature or inadequate nutrition might be subtle enough during maturation to reduce fecundity at times without altering body length of the fish. However, it is unlikely that differences in fecundity of the magnitude noted between Alsea and Scott Creek steelhead could be produced by environmental conditions without also affecting size of fish at maturity. Hence,

some insight into the cause of the fecundity differences might be gained by comparing growth rate of steelhead of similar age from the two areas.

In order to compare size at maturity of Alsea steelhead with fish from California waters it was necessary to use data presented by Shapovalov and Taft (1954) for steelhead from Waddell Creek located some 4 miles from Scott Creek. Length data on Waddell fish were collected from the 1933–34 to 1940–41 spawning seasons. Alsea fish were sampled from the 1957–58 to the 1964–65 spawning runs. The comparisons were felt to be valid even though samples were collected in different years on the assumption that normal variations in seasonal marine growth are covered in the 8- and 9-year periods of sampling spawning runs in the two streams. To the extent that annual variations are not covered by the sampling periods the comparisons are vulnerable. Any long-term trend in marine environmental conditions would also invalidate the comparisons.

Growth comparisons between steelhead from the two streams were not conclusive since fish in some life-history patterns from Waddell were longer and those in others were shorter in mean length than Alsea fish (Table I). Alsea steelhead having a single year of freshwater growth were hatchery fish released as smolts; the balance of the Alsea steelhead were wild fish. Male jack steelhead of hatchery origin from Alsea were considerably larger on the average than those from Waddell Creek. Wild Alsea 3/2 fish of both sexes were considerably smaller. A statistical comparison of mean seasonal average lengths of fish in all life-history patterns with an adequate number of years suggested that growth of steelhead from the two streams was similar. The hypothesis that the means of seasonal average lengths were equal could not be rejected for any life-history group ($P = 0.05$). Unfortunately, as lengths of individual fish were not given by Shapovalov and Taft, more accurate comparisons could not be made. The magnitude of differences in mean length given in Table I strongly suggests that fish of certain life-history patterns are different in growth rates but mean growth rates of the two populations appear similar. Thus, the large difference in fecundity noted between steelhead from

TABLE I. Mean fork lengths (cm) at maturity according to life-history patterns of steelhead trout from Waddell Creek, California (Shapovalov and Taft, 1954), and Alsea River, Oregon; sample size in parentheses.[a]

Location	1/1	2/1	1/2		2/2		3/2		1/2S.3		2/2S.3	
Waddell Creek	38.5 (106)	45.3 (641)	65.0 (98)	65.4 (34)	66.7 (497)	70.4 (316)	69.4 (86)	72.9 (27)	73.5 (2)	71.0 (2)	69.4 (20)	68.2 (10)
Alsea River	44.9 (77)	46.4 (20)	64.4 (274)	67.4 (269)	64.5 (124)	68.7 (106)	63.9 (29)	5.65 (12)	73.1 (94)	72.4 (15)	72.9 (31)	68.6 (2)

[a]Numerals on the left of the oblique indicate years of freshwater growth; on the right, years of saltwater growth.

Scott Creek and Alsea River cannot be attributed to increased growth rate of the southern population. If warmer ocean temperatures or better food supply during maturation favorably influenced fecundity of Scott Creek steelhead, it was not apparent from available data.

The possibility should be considered that the fecundity differences noted above reflect genetic divergence within the species. Neave (1948) discussed the relation of Pacific salmon fecundity to mortality factors acting upon different species during the life cycle. He found that species with high fecundity inhabit the more hazardous environments when in fresh water. In a rigorous environment where mortality is high, the highly fecund individual could be more successful in replacing itself because its offspring are more abundant. Thus, an evolutionary trend in the direction of increased fecundity is encouraged. Svardson (1949) presented a similar theoretical explanation for fecundity differences. Overpopulation does not necessarily result from natural selection of the more fecund individual because competition and environmental factors frequently control survival of a year-class within a wide range of egg potential. The theory operates as well within a single species. As steelhead stocks near the southern portion of their range are undoubtedly subjected to hazardous freshwater conditions more frequently than those in the northern portion, a trend toward higher fecundity is not unlikely.

Whatever the cause of the high fecundity of steelhead in the southern portion of their range (probably both environment and heredity are involved), the ecological advantages are obvious. High fecundity coupled with a relatively high percentage of repeat spawning (Withler, 1966) undoubtedly allows the populations to survive periods of adverse environmental conditions. Indeed, the wide flexibility in fecundity and life-history patterns is probably one factor which has allowed the steelhead trout to extend southward beyond the geographic range of most Pacific salmon.

ACKNOWLEDGMENTS

Sincere thanks are expressed to James L. Fessler for assistance in collection of data and to Harry H. Wagner for access to unpublished data on age of Alsea steelhead.

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Limnetic Larval Fish in Northern Wisconsin Lakes[1,2]

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ABSTRACT

The open water of two northern Wisconsin lakes was sampled for larval fish at night with fine-mesh conical townets. Those collected were identified to genus or species and enumerated. The majority of larval fish were captured in the limnetic region but a few never strayed from the littoral region.

The seasonal changes of the limnetic species were similar for the two lakes and 3 years of study. Their abundance varied greatly from year to year but yellow perch, sunfish, and black crappies always dominated.

INTRODUCTION

Field studies concerning naturally hatched freshwater fish in open water or limnetic regions are few. The most comprehensive collection of such fish in North America is that of Fish (1932) in Lake Erie. Battle and Sprules (1960) reported that a townet was needed to collect larval goldeye, *Hiodon alosoides*, in the surface waters of Lake Claire and Lake Mamawi, Alberta; Miller (1960) reported that a townet was used to collect larval gizzard shad, *Dorosoma cepedianum*, in Buckeye Lake, Ohio. Backiel (1958) compared the species composition and abundance of larvae in the lentic and lotic regions of the middle Vistula River of Poland. Many investigators have relied upon hatcheries to provide the necessary specimens for examination rather than collecting them in lakes after hatching naturally.

The present study was undertaken to determine which species utilize the limnetic regions of two northern Wisconsin lakes. It was found that the majority of species regularly disperse into the open-water region after hatching and can be collected there at night with fine-mesh townets.

LAKES

Two lakes, Little John and Erickson, in northern Wisconsin were studied. Their limnetic regions are defined here as that region which is at least 3 m deep with no aquatic plants growing into it, although there may be algae covering the bottom. Throughout spring and summer the central limnetic region remains the most extensive habitat. The variety of larval fish found

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after dark in this habitat partially reflects the diversity of species within the lakes. Spring- and summer-spawners and nest-builders and non-nest-builders are represented. Muskellunge, largemouth and smallmouth bass, brook sticklebacks, and central mudminnows were conspicuously absent from the collection.

May, June, and July, the time when most larvae are present in limnetic regions, belong to the "warming phase" for lakes in central North America (McCombie, 1959). Spring warm-up rates of the study lakes undoubtedly differ, for Scott (1964) has shown that the rate of increase of mean lake temperatures during April of small lakes in Vilas County, Wisconsin, varies inversely with mean depths. This relationship substantiates the meagre surface temperature data in Fig. 1 which indicates that each year during May, Erickson Lake (mean depth 2.8 m) heats up faster than Little John Lake (mean depth 3.5 m). These lakes are essentially homiothermal through April and May during which time surface temperatures should be directly related to mean temperatures.

Little John Lake

Little John Lake lies in central Vilas County, Wisconsin (T41N, R7E, Sec. 20, 29). Its area is 67.2 ha (Fig. 2). The bottom is hard in most areas. Wilson (1935) discussed the relationship of Little John Lake to several nearby lakes and indicates that it is not a typical lake of Vilas County because it has hard water and is supplied by seepage. It is considered a hardwater lake in northern Wisconsin, having a total alkalinity of 46 ppm (Wilson, 1935).

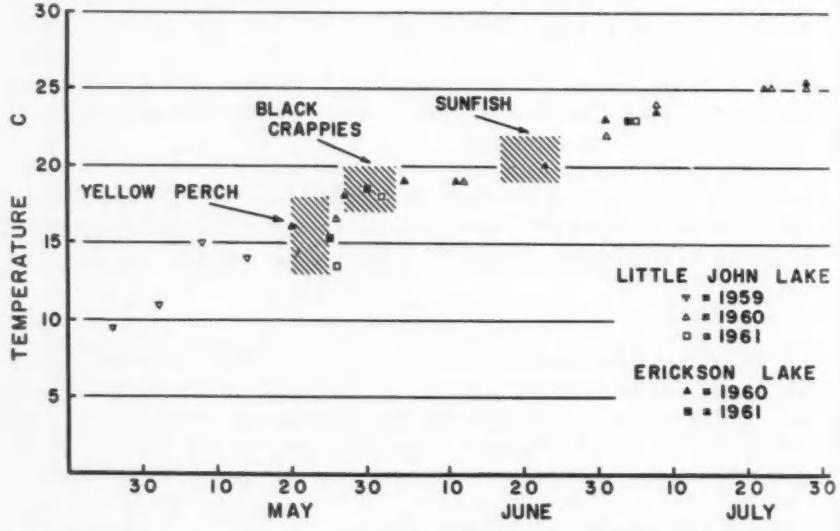

FIG. 1. Surface water temperatures of Little John Lake and Erickson Lake during the period of study. Hatched areas indicate the range of dates and temperatures when dominant species first appeared in the limnetic region.

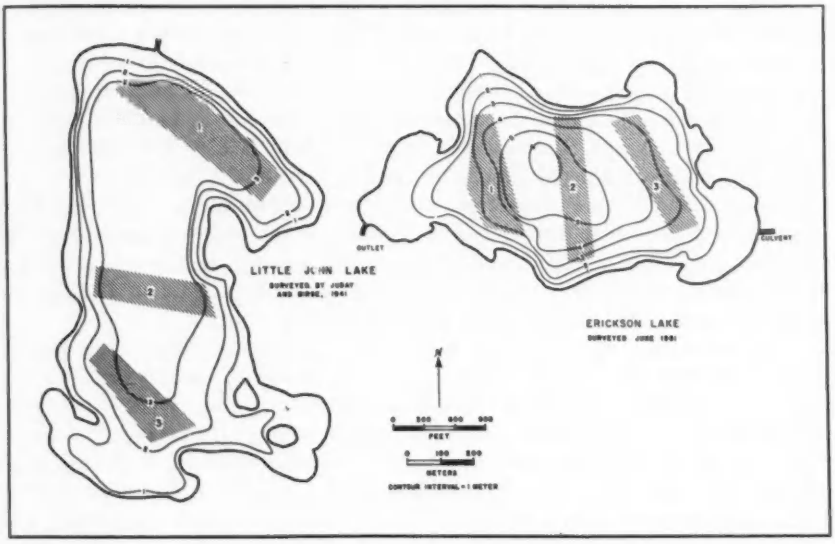

FIG. 2. Hydrographic maps of Little John Lake and Erickson Lake. Hatched areas indicate sampling courses and numbers identify the stations.

A thermocline develops after May except during periods of strong winds.

Daphnia spp. are the predominant zooplankters in the lake but large numbers of *Chaoborus* spp. larvae are collected at times.

ERICKSON LAKE

Erickson Lake lies in southern Vilas County, Wisconsin (T40N, R7E, Sec. 16). Its area is 48.1 ha as calculated from United States Department of Agriculture aerial photographs. It is one of a short connecting series of seepage lakes. Figure 2 shows the hydrography derived from soundings made with a Bendix depth recorder. Some areas show a "false bottom" owing to the accumulation of soft organic materials. Having a total alkalinity of 21 ppm, it is considered to be a medium hardwater lake in Vilas County (Wilson, 1935). Temperature stratification is similar to that of Little John Lake.

Daphnia spp. and *Holopedium gibberum* are the predominant small zooplankters whereas amphipods and larvae of *Chaoborus* spp. are the larger forms collected.

SAMPLING PROCEDURES

It had been observed that marine larval fish were collected in greater numbers at night than by day (Bridger, 1956; Isaacs, 1964). Testing this observation with net A in Little John Lake showed that, here too, more and older larval yellow perch could be collected at night than during the day.

The lakes were sampled at night in a stratified random manner and three conical townets (designated A, B, and C) with different meshes were used to sample larval fish (Faber, MS, 1963). The rate of plankton accumulation in the plankton bucket allowed the tows to be 3–4 min long at an average speed of 40 m/minute. At each of the three stations in the two lakes three replicate tows with nets A and B were taken at both the surface (0–1 m) and bottom (3–4 m) and directed perpendicular to the long axis of the lake (Fig. 2).

Nets A and B were towed from a wooden boom on the port side of a 12-ft boat. A lazy line, that constricted the codend of the net, was used to ensure that bottom samples would not become contaminated with larvae inadvertently caught in surface waters. Net C was towed between two 12-ft boats. Only five surface tows were taken with net C each night.

As taken from the plankton bucket, the collections consisted of several distinct groups of animals: Microcrustacea, consisting mainly of *Daphnia* spp. and *Holopedium gibberum*; miscellaneous macroplankton, such as larvae of *Chaoborus* spp., amphipods, mayflies, and Tendipedidae larvae; and larval fish. The collections were preserved in 5% formalin solution. A 10-inch glass pie plate set over black and white backgrounds was used to handpick the fish from the plankton. Over 57,000 larval fish were collected, preserved, and identified during the 3-year study. Adult fish were sampled at night with a 220 v a-c shoreline boom shocker.

DOMINANT LARVAL FISH

Larval fish collected in the limnetic region were divided for convenience into dominant and rare species. The dominants were taken at times in considerable numbers, whereas only a few individuals of rare species were ever collected. Descriptions by Fish (1932), Morgan (1951, 1954), Balon (1959), and Norden (1961) were used to identify the dominant limnetic larvae, i.e. yellow perch, black crappie, and sunfish.

The seasonal change in species composition was similar for the two lakes and 3 years of study. Larval yellow perch appeared first in late May, black crappies in early June, and sunfish in late June. Their initial appearance into the limnetic region varied only about a week between the 3 years. Temperature data in Fig. 1 shows that larval yellow perch appeared when surface water temperatures ranged between 13 and 18 C, black crappies between 18 and 20 C, and sunfish between 19 and 22 C.

The abundance of larvae was extremely variable from year to year and the cause is undoubtedly complex owing to a multiplicity of factors relating to both abundance and net selectivity. Nevertheless, each year yellow perch were always most abundant, sunfish next, and black crappie least abundant.

Yellow Perch

Each year larval perch were caught in varying numbers in the limnetic region from late May until early July (Fig. 3). They were collected for about 1

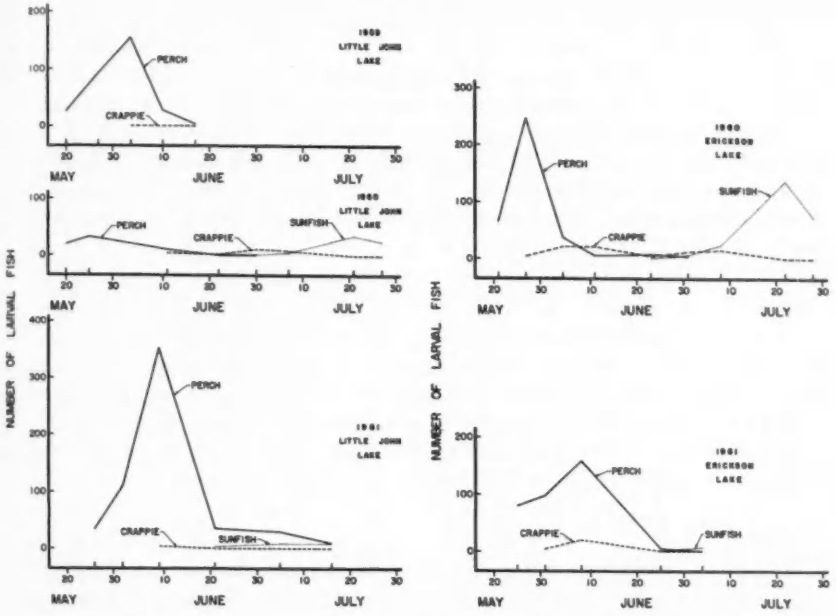

FIG. 3. Seasonal abundance of the dominant larvae in the limnetic regions of Little John and Erickson lakes. Vertical lines along the horizontal axis represent sampling dates. Values are geometric means of replicate tows corrected for differences in length of tow and diameter of net mouth.

week in increasing numbers up to a maximum, then in decreasing numbers. Variations are evident between different years and different lakes.

In Little John Lake maximum numbers appeared a week later in 1961 than in 1959 (Fig. 3). A strong peak was not evident in 1960, but one may have occurred during the first week of June when samples were not taken. In Erickson Lake, the 1960 peak, in late May, was earlier than and almost twice the height of that recorded in 1961.

BLACK CRAPPIES

Larval black crappies were never collected in significant numbers in either lake (Fig. 3), presumably because adults were never abundant. These larvae first appeared during the first half of June and continued in small numbers through most of July. In Erickson Lake there were two small but distinct periods of abundance in 1960, early June and early July. In 1961 a single peak occurred, about a week earlier in Erickson Lake than in Little John Lake. This is consonant with the warming trends in the two lakes and the resulting phenology.

Sunfish

Although both *Lepomis gibbosus* and *L. macrochirus* are present in the lakes, less than 1% of the sunfish adults could be positively identified as the former species. Thus the following discussion relates mainly to bluegill sunfish.

Larval sunfish appeared during the third week of June but only in 1960 was sampling carried out long enough into summer to present any semblance of their seasonal abundance (Fig. 3). In both lakes numbers were small for 4 weeks before peaks occurred. Both yellow perch and black crappies showed peaks after only about 1 week.

RARE LARVAL FISH

The rare larval fish, compared to the dominants, were collected in the limnetic region in small numbers. Several of the group appear to be truly limnetic for a time but others were observed in the littoral region in greater abundance and should be considered predominantly littoral larvae. Reighard (1890), Stewart (1926), Fish (1932), Balinsky (1948), and Winn and Miller (1954) were useful references to identify the genera of rare larvae.

Burbot

Early spawning coupled with a short incubation period results in burbot being one of the first larvae to appear in the limnetic region. In Little John Lake, larvae were not collected in 1959 and only in small numbers in 1960 and 1961 (Table I).

Fish's (1932) records of larval burbot from Lake Erie suggest they are limnetic there (depths from 5 to 60 m). In coastal waters all common gadoids live pelagically for a time after hatching. Larval burbot were collected in both surface and bottom waters of Little John Lake, thus they appear to be limnetic in this lake.

Walleye

The annual appearance of walleye larvae suggests that walleye eggs hatch during May in these lakes (Table I). The presence of older larvae in June and their capture in both surface and bottom waters indicate that larval walleyes are limnetic in these two lakes. These facts substantiate Eschmeyer's (1948) theory on the behavior of newly hatched walleyes in a Michigan lake. He states that "Although not substantiated by collections made in Lake Gogebic, the suggestion is made that the fry move into open water of the lakes shortly after hatching and lead a pelagic existence until a length of nearly an inch or more is attained." Houde (MS, 1965) also observed them to be limnetic in Oneida Lake, New York.

Mottled Sculpin

Larval sculpins were erratically collected during May and June (Table I). The adult mottled sculpin is a fish of rivers and rocky bottoms but it appears

TABLE I. The seasonal occurrence and abundance of rare larval fish in the limnetic regions of Little John Lake and Erickson Lake.[1] Values are geometric means of replicate tows corrected for differences in length of tow and diameter of net mouth.

Little John Lake

	1959					1960								1961					
	May		June			May		June		July				May	June			July	
	20	27	3	10	17	21	26	12	23	1	8	22	28	26	1	9	21	5	16
Burbot	–	–	–	–	–	0.1	0.1	–	–	–	–	–	–	+[a]	+	–	–	–	–
Walleye	1.3	3.2	2.8	–	–	0.3	0.2	–	–	–	–	–	–	0.1	+	0.1	+	–	–
Sculpin	–	1.2	–	0.9	0.2	–	–	–	–	–	–	–	–	–	0.1	+	+	–	–
Sucker	–	–	13.2	8.9	0.2	–	–	0.2	8.9	1.5	0.7	–	–	–	–	0.3	–	–	+
Darters	–	–	5.0	2.3	0.5	–	–	0.2	+	0.2	0.7	0.2	–	–	–	2.3	0.4	+	0.1
Minnows	–	–	–	–	0.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rock bass	–	–	–	–	–	–	–	–	0.8	0.1	0.1	–	–	–	–	–	0.2	0.2	+

Erickson Lake

	1960									1961				
	May		June			July				May		June		July
	21	27	4	11	23	1	8	22	28	25	31	8	25	4
Walleye	0.6	1.1	0.2	–	–	–	–	–	–	0.5	0.3	–	–	–
Sculpin	–	+	–	–	+	–	–	–	–	–	–	0.1	–	–
Sucker	–	0.2	3.3	1.3	–	–	–	–	–	–	0.6	21.2	–	+
Minnows	–	–	–	0.1	0.2	–	–	–	–	–	–	–	0.6	0.5
Rock bass	–	–	–	–	0.7	0.1	0.1	0.2	–	–	–	–	–	0.5

[a] + = <0.1 fish per haul.

the larvae are not so restricted. Taranets (1941) believes that all larval Cottidae are pelagic for a time before they settle down to the bottom. Recently, Heard (1965) has reported larval *Cottus aleuticus* but not *C. cognatus* to be limnetic in Brooks Lake, Alaska. The townet data from Erickson and Little John lakes suggest that larval mottled sculpins are limnetic for a short time.

Common White Sucker

Sucker larvae were on occasion the most abundant of the rare species. They were first collected in late May in Erickson Lake and in June in Little John Lake (Table I), observations which appear to be related to the faster warmup of Erickson Lake. The appearance of early stages as late as July suggests that some spawning occurs in these lakes even in late June.

Stewart (1926) has given an excellent account on the early behavior of larval suckers in New York State rivers. He repeatedly observed them within inches of the surface in moderate currents and learned they were rarely found in quiet pools but rather in areas where streams enter deep, quiet stretches. Large numbers of larval suckers were observed in both lakes schooling in very shallow water (2–5 cm) near shore. The townet data show they can regularly be caught in the limnetic region after dark. Apparently larval suckers are predominantly littoral larvae and to a lesser extent limnetic in these lakes.

Darters

At least three species of larval darters were collected in Little John Lake; logperch, *Percina caprodes*, is known to be one of them but at least two smaller forms, *Etheostoma* spp., were recognized on the bases of their pigmentation and relationship between length and morphological stage.

Larval darters were collected from early June through most of July (Table I). Larval logperch were collected in June while the smaller forms appeared in July. Fish's (1932) records indicate that logperch are limnetic in Lake Erie (depths from surface to bottom). In Little John Lake they were caught in both surface and bottom waters, thus they appear limnetic there. The smaller forms were collected in less abundance.

Minnows

Larval minnows, which appeared in late June and throughout July (Table I), were not identified to species. Fish's (1932) records indicate that the lake emerald shiner, *Notropis atherinoides*, was the only limnetic larval minnow in Lake Erie. Larval minnows were observed to form schools along the shores of Erickson and Little John lakes. The townet data indicate that only stray individuals wander into open water at night.

Rock Bass

Larval rock bass were consistent in their appearance each year, being collected from late June through July (Table I). Fish (1932) suggests they

are littoral larvae in Lake Erie. In Erickson and Little John lakes, larval rock bass appear to be limnetic or partially so.

DISCUSSION

The movements of recently hatched fish, especially in the numerous lakes in glaciated North America, have not been thoroughly studied. It has been shown by previous investigations (Hart, 1930; Pritchard, 1930; Carbine, 1942; Battle and Sprules, 1960) that fish do not commonly spend their entire life in one region of a lake. Lakes can be objectively divided into two habitats, the deep open water and shallow water; thus larval fish collected in the former region can be designated limnetic whereas those collected in the latter can be designated littoral larvae. Since muskellunge, largemouth and smallmouth bass, sticklebacks, and mudminnows were never collected with townets in the present study, it is assumed they have littoral larvae that do not wander into limnetic regions.

An important concept emerges — many species move into the limnetic region after hatching and can be found there for several weeks. This behavior is quite different from the well-known habits of bullheads, dogfish, largemouth bass, suckers, and certain minnows. The young of these latter species leisurely move along the littoral region in tight aggregations (Richardson, 1913). It appears that littoral larvae prefer not to lose sight of the lake bottom while limnetic larvae may.

Several plausible explanations exist as to the reason why young fish move into limnetic regions. Most aquatic as well as terrestial organisms have a dispersal phase at some time during their life (Andrewartha and Birch, 1954), so this could illustrate dispersion away from the spawning area. Or they might be wandering in search of suitable food, since "avoidance of the shore" (Ruttner, 1963) sometimes prevents an abundance of planktonic crustaceans within the littoral region. Another possibility lies in protection provided to the larvae. Predators would have a difficult time to recognize the transparent larvae from among the limnetic Crustacea. Finally, Andrewartha and Birch suggest that the movements of thrips from flower to flower could be the result of an innate "wanderlust." Possibly some larval fish possess it too.

Recent investigations by the author in Lake Huron suggest that a lake's hydrography is an important factor in the ecology of larval fish. In South Bay, an inlet of Lake Huron, the majority of limnetic larvae are found in the top 10 m of the limnetic region.

If certain larvae disperse into the limnetic region for a period after hatching and some do not, then determining ecological conditions necessary for successful year-classes becomes quite complex. The environmental conditions necessary for good survival among limnetic larvae will not be the same as those among littoral larvae. In addition there are inherent temporal variations owing to the staggered appearance of different species throughout spring and their exposure to irregular seasonal variations of plankton. Thus, there is

apparently little similarity in ecological conditions experienced by any two species during their first several weeks of life.

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Effect of a Partial Loss of Scales and Mucous on Carbohydrate Metabolism in Rainbow Trout (*Salmo gairdneri*)[1]

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ABSTRACT

This study was undertaken to determine what part partial scaling and partial desliming might play in the survival of trout. Carbohydrate metabolism in these trout was studied and in addition, hemoglobin levels and red cell volumes were studied to serve as indicators of osmotic shifts of water.

Increases in lactate were minimal and occurred during the first few hours of holding after the removal of $\frac{1}{8}$th to $\frac{1}{4}$ of the scales. There were slight changes in hemoglobin levels and red cell volumes which appeared to coincide with activity as reflected by lactate levels. There was a three- to fourfold increase in the blood glucose level of partially scaled fish. Liver glycogen levels dropped to $\frac{1}{3}$th of the air-dipped control value for fish that had been $\frac{1}{8}$th scaled and held in holding baskets for a period of 140 hr. Only one mortality occurred in all the experiments.

The following conclusions were reached. Partial loss of scales or mucous does not result in the death of rainbow trout (*Salmo gairdneri*). Partial scaling or desliming of the fish was accompanied by a significant increase in blood glucose ($p < 0.05$).

INTRODUCTION

Severe muscular exercise causes death in certain fish under certain conditions (von Buddenbrock, 1938; Secondat and Diaz, 1942; Milne and Ball, 1956; Black, 1957c; and Parker and Black, 1959). Von Buddenbrock and other workers believed that the primary cause of death was the flooding of sensitive tissues by lactic acid liberated by glycolysis from muscle stores. In experiments reported by Black (1957c) a few scales were lost during the forced exercise. It is possible that osmotic inflow may have contributed or even caused death.

The present work was undertaken to determine whether partial loss of scales or loss of mucous (deslimed) would cause death in freshwater rainbow trout. From a casual observation made by one author in 1954, blood glucose was found occasionally to be 10 times the normal level in those fish that had been injured and scaled during line fishing. Similar high values were reported by Kiermeir (1939) in her extensive study of glucose metabolism in fish. In this series of experiments carbohydrate metabolism was studied to monitor the blood lactate levels and to follow changes in blood glucose associated with injury.

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[2]Deceased March 11, 1967.

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MATERIALS AND METHODS

The experiments were carried out on hatchery-raised domestic stock rainbow trout during the summer months of 1963 and 1964 at the Trout Hatchery, operated by the Fish and Game Branch of the Department of Recreation and Conservation, Summerland, British Columbia. The stock used in 1963 were obtained from Oregon and the fish used in 1964 were obtained from Washington state. The fish were approximately 1.5 years old.

The trout were hatched and reared at Summerland. The water temperature was 11.5 C, the water being supplied from an artesian source. Fish were fed on Clark's commercial pelletted feed. During 1964, the trout were treated with sulfamerizine to control furunculosis. The trout were held in covered hatchery troughs.

Some of the control fish were sampled immediately from the stock troughs whereas others were held in covered hatchery baskets for various periods up to 140 hr. Control and experimental fish (7 to 13 in each group) were anaesthetised by immersing the fish in a solution of tricaine methanesulfonate (MS 222, Sandoz) for 45–55 sec. The concentration of the anaesthetic was 0.5 g of MS 222 dissolved in 1 U.S. gal of water (3.8 liters). Black and Connor (1964) showed that MS 222 did not influence significantly the levels of hemoglobin, lactate, or glycogen from either blood or muscle.

Scaling was carried out by removing the scales from the tail region. Two degrees of scaling were employed, namely the removal of scales from $\frac{1}{6}$th of the total body area and removal of scales from $\frac{1}{4}$ of the total surface area of the body.

Removal of slime was accomplished by scraping the slime from an anaesthetised fish with a scalpel and also by scraping after treatment with rock salt. Rock salt was applied to the fish and then wiped off with rough towelling. Desliming was nearly complete but there was no obvious loss of scales. All mucous was removed from the pectoral fins back. After scaling and desliming, the fish were held without food in the troughs for varying lengths of time.

Blood was drawn from the heart into a Luer syringe while the fish respired in water. Heparin (Connaught Laboratories, 1000 I.U. per cc) was used as the anticoagulant.

In 1963, the acid hematin method as given by Hawk et al. (1954) was used to determine hemoglobin. In 1964, hemoglobin was determined by the pyridine hemochromogen method as described by Collier (1944) and modified by Klawe et al. (1963).

Another sample of blood was deproteinised in zinc and barium hydroxide. An aliquot of the filtrate was analysed for glucose the following day using the method of Nelson and Somogyi as given in Hawk et al. (1954). Lactate analyses were carried out on an aliquot of the remainder of the filtrate according to the method of Barker and Summerson as given in Hawk et al. (1954).

A third sample of blood was taken in 1964. This was centrifuged at 12,000–14,000 rpm for 1 min and the hematocrit read immediately.

In 1964, livers were removed and placed in a freezing mixture of dry ice and ethanol. The liver was then weighed and glycogen was determined on KOH digests by the anthrone method of Carroll et al. (1956), after precipitation in 65% ethanol (Connor et al., 1964).

RESULTS AND DISCUSSION

Hemoglobin

During 1963, the acid hematin method was used to determine the hemoglobin content of the blood. As demonstrated by Anthony (1961) the acid hematin method is far from being dependable when applied to fish blood.

The average control value taken in 1963 was 10.9 g/100 ml blood. The various levels for control fish and $\frac{1}{6}$th-scaled are illustrated in Fig. 1 and for $\frac{1}{4}$-scaled fish in Fig. 2. There would not appear to be any significant difference between the scaled fish and the controls. However, the levels were much lower in scaled

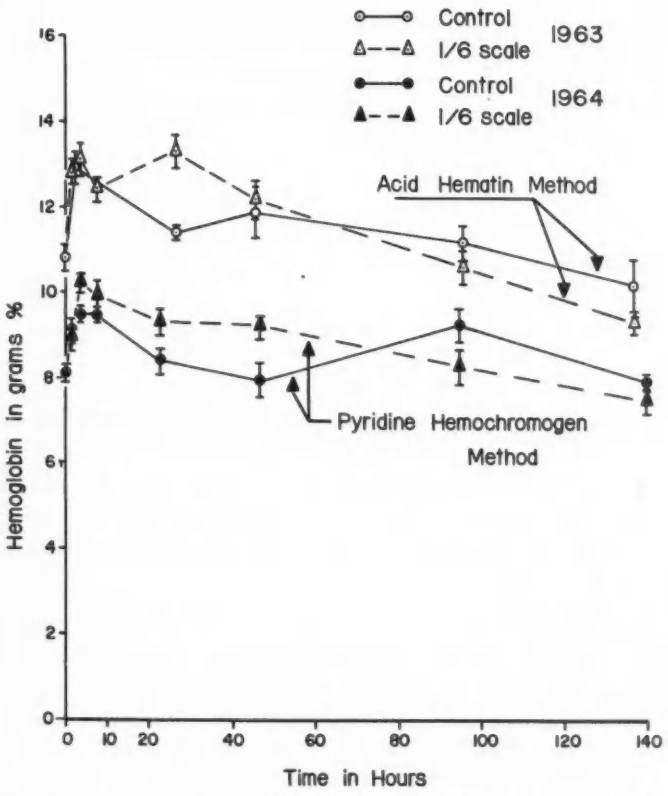

FIG. 1. Changes in hemoglobin in 18-month-old rainbow trout (*Salmo gairdneri*) after removal of $\frac{1}{6}$th of body scales and recovery.

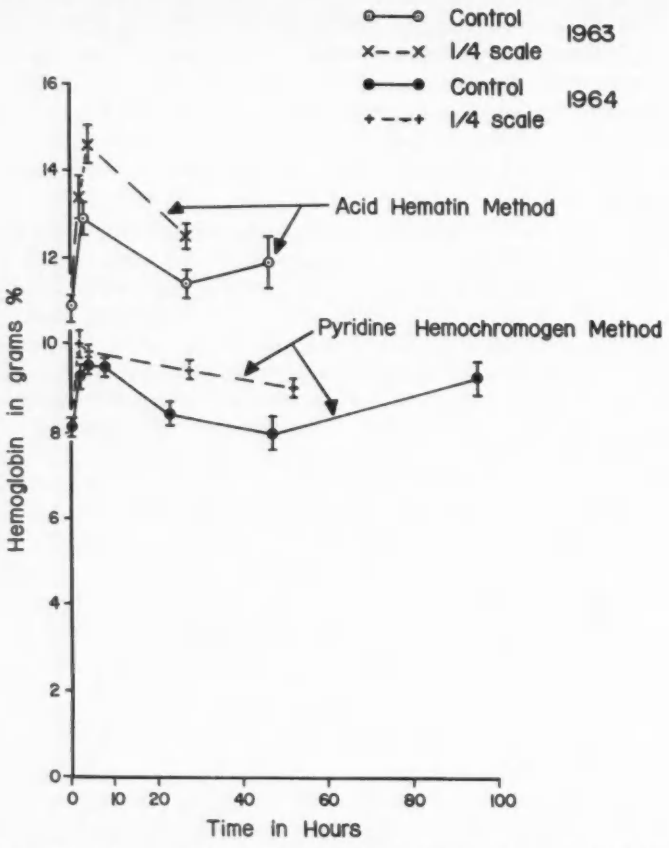

FIG. 2. Changes in hemoglobin in 18-month-old rainbow trout (*Salmo gairdneri*) after removal of $\frac{1}{4}$ of body scales and recovery.

fish than in the controls after 96 and 140 hr of recovery. For fish that had been $\frac{1}{4}$ scaled, the hemoglobin values were higher at the 8th and 24th hr after scaling. Experiments were not carried beyond a holding period of 24 hr in 1963 and 52 hr in 1964.

The pyridine hemochromogen method was compared to the acid hematin method with the blood of five fish during the summer of 1964. The average hemoglobin value of the five samples using the pyridine hemochromogen method was 9.134 g/100 ml, whereas the average of the same samples determined by the acid hematin method was 10.926 g/100 ml. Using the ratio of the two averages, equivalent acid hematin averages for controls in 1964 was 9.7 g/100 ml compared with an average of 10.8 g/100 ml for airdipped controls carried out in 1963. This difference is no greater than that reported in earlier studies by Black (1957a).

The hemoglobin values using the pyridine hemochromogen method are pitched at about 3 g less than the values obtained using the acid hematin method. The values for $\frac{1}{6}$th-scaled fish in 1964 (Fig. 1) are about the same for both scaled and control fish. However, as in 1963, the averages are less for scaled fish after 96 and 140 hr of recovery. For $\frac{1}{4}$-scaled fish the hemoglobin values are consistently higher than the controls (Fig. 2). The hemoglobin levels for fish that had been deslimed show values that are higher than the controls at the 4th hr of holding.

Red Cell Volume (Hematocrit)

Comparisons of red cell volume (hematocrit) are illustrated in Fig. 3 for $\frac{1}{6}$th- and $\frac{1}{4}$-scaled fish studied in 1964. The hematocrits were consistently higher in the scaled fish compared with the controls up to 48 hr but there was no difference in the red cell volume at 96 and 140 hr after scaling.

Lactate

The course of changes in blood lactate for trout that had been $\frac{1}{6}$th-scaled is displayed along with the control values in Fig. 4. There is only one significant increase ($p < 0.05$), that is the peak exhibited at the 4th hr after scaling for the 1964 data. The increased lactate and the recovery values are similar

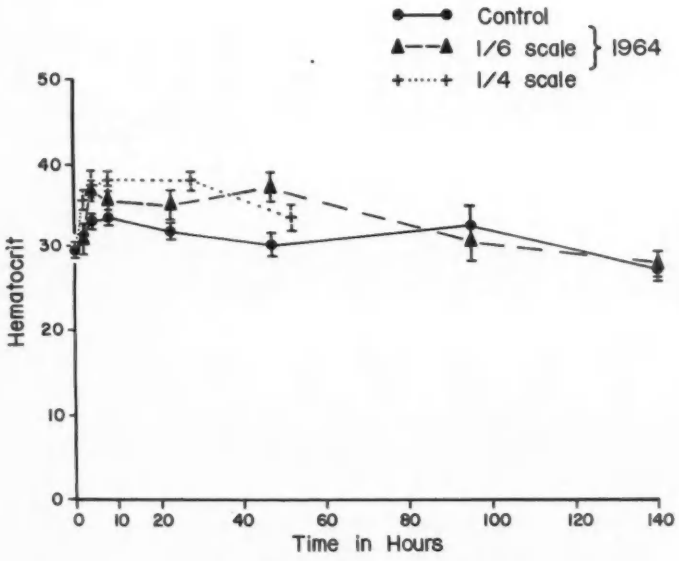

Fig. 3. Changes in hematocrit in 18-month-old rainbow trout (*Salmo gairdneri*) after partial scaling and recovery.

TABLE I. Average body weights, hemoglobins, red cell volumes, blood lactate, blood glucose, and liver glycogen for $\frac{1}{6}$th-scaled and control rainbow trout, *Salmo gairdneri* (1964).

Condition		Body weights (g)	Hemoglobin (g/100 ml)	Red cell volume (%)	Blood lactate (mg/100 ml)	Blood glucose (mg/100 ml)	Liver glycogen (%)
Air-dipped controls	Mean ± S.E.	232.1±12.90	8.11±0.258	29.8±1.01	7.13±2.326	53.36±3.441	3.70±0.522
	S.D.	46.54	0.930	3.64	8.389	12.409	1.882
	Range	150–313	6.85–9.41	25.0–36.5	0.91–30.1	40.18–74.90	0.64–6.08
	n	13	13	13	13	13	13
2-hr unscaled controls	Mean±S.E.	265.0±6.48	9.14±0.306	31.3±1.13	6.64±1.287	58.57±4.885	4.16±0.601
	S.D.	23.38	1.062	3.92	4.459	16.820	2.168
	Range	239–323	7.33–11.60	23.9–36.7	1.01–18.1	26.67–93.00	1.11–8.71
	n	13	12	12	12	12	13
4-hr unscaled controls	Mean±S.E.	263.0±13.76	9.50±0.193	33.1±1.14	7.96±1.694	74.89±10.180	3.65±0.450
	S.D.	51.49	0.724	4.28	6.340	39.093	1.684
	Range	198–379	7.82–10.50	21.0–38.5	0–26.8	32.48–188.70	0.05–4.55
	n	14	14	14	14	14	14
95-hr unscaled controls	Mean±S.E.	264.0±18.20	9.26±0.440	32.8±2.36	5.21±1.121	47.11±2.944	1.30±0.275
	S.D.	54.61	1.247	6.70	3.173	8.327	0.779
	Range	200–374	7.34–11.30	24.4–47.5	0–8.23	34.4–66.36	0.59–3.15
	n	9	8	8	8	8	8
140-hr unscaled controls	Mean±S.E.	267.6±13.85	7.92±0.244	27.5±1.56	4.61±1.007	53.29±5.662	0.98±0.141
	S.D.	41.56	0.734	4.70	3.022	16.988	0.422
	Range	207–328	6.95–9.05	16.7–33.3	1.18–11.0	35.25–91.25	0.40–1.70
	n	9	9	9	9	9	9
2-hr $\frac{1}{6}$th scaled	Mean±S.E.	260.0±13.65	8.99±0.448	30.9±2.16	6.96±1.185	82.26±9.930	3.60±0.531
	S.D.	38.62	1.26	6.12	3.352	28.086	1.500
	Range	203–335	6.61–9.96	20.5–37.9	3.70–12.90	32.85–130.10	2.10–5.75
	n	8	8	8	8	8	8
4-hr $\frac{1}{6}$th scaled	Mean±S.E.	272.0±7.20	10.20±0.20	37.1±1.04	20.3±4.40	123.10±9.41	3.02±0.444
	S.D.	41.75	0.65	3.29	13.940	29.76	1.405
	Range	231–312	9.11–11.50	33.3–44.7	4.74–45.20	91.41–165.70	0.15–4.18
	n	10	10	10	10	10	10
95-hr $\frac{1}{6}$th scaled	Mean±S.E.	290.7±16.86	8.31±0.419	30.6±2.36	9.28±2.905	96.27±16.616	1.06±0.281
	S.D.	53.33	1.327	7.49	9.188	52.547	0.889
	Range	237–405	5.23–9.63	13.2–38.7	0.649–30.7	37.33–185.50	0.17–2.86
	n	10	10	10	10	10	10
140-hr $\frac{1}{6}$th scaled	Mean±S.E.	286.0±13.11	7.55±0.390	28.0±1.60	5.93±1.151	32.52±3.108	0.52±0.129
	S.D.	37.09	1.105	4.53	3.257	8.790	0.366
	Range	240–338	6.68–8.98	18.4–33.3	1.33–10.30	19.04–42.52	0.08–1.01
	n	8	8	8	8	8	8

TABLE II. Average body weights, hemoglobins, red cell volumes, blood lactate, blood glucose, and liver glycogen for $\frac{1}{3}$-scaled and control

TABLE II. Average body weights, hemoglobins, red cell volumes, blood lactate, blood glucose, and liver glycogen for ¼-scaled and control rainbow trout, *Salmo gairdneri* (1964).

Condition		Body weights (g)	Hemoglobin (g/100 ml)	Red cell volume (%)	Blood lactate (mg/100 ml)	Blood glucose (mg/100 ml)	Liver glycogen (%)
Air-dipped controls	Mean ± S.E.	232.1 ± 12.90	8.11 ± 0.258	29.8 ± 1.01	7.13 ± 2.326	53.36 ± 3.441	3.70 ± 0.522
	S.D.	46.54	0.930	3.64	8.389	12.409	1.882
	Range	150–313	6.85–9.41	25.0–36.5	0.913–30.10	40.18–74.90	0.64–6.08
	n	13	13	13	13	13	13
2-hr unscaled controls	Mean ± S.E.	265.0 ± 6.48	9.14 ± 0.306	31.3 ± 1.13	6.64 ± 1.287	58.57 ± 4.855	4.16 ± 0.601
	S.D.	23.38	1.062	3.92	4.459	16.820	2.168
	Range	239–323	7.33–11.60	23.9–36.7	1.01–18.10	26.67–93.00	1.11–8.71
	n	13	12	12	12	12	13
4-hr unscaled controls	Mean ± S.E.	263.0 ± 13.76	9.50 ± 0.193	33.1 ± 1.14	7.96 ± 1.694	74.89 ± 10.180	3.65 ± 0.450
	S.D.	51.49	0.724	4.28	6.340	39.093	1.684
	Range	198–379	7.82–10.5	21.0–38.5	0–26.80	32.48–188.70	0.05–4.550
	n	14	14	14	14	14	14
23-hr unscaled controls	Mean ± S.E.	286.6 ± 10.02	8.39 ± 0.319	32.0 ± 1.00	7.85 ± 2.353	55.25 ± 3.474	3.03 ± 0.777
	S.D.	30.08	0.959		7.061	10.422	2.332
	Range	243–334	7.34–10.30	26.8–37.1	0.66–10.60	41.65–77.10	0.36–7.33
	n	9	9	9	9	9	9
47-hr unscaled controls	Mean ± S.E.	274.5 ± 10.98	7.94 ± 0.429	30.3 ± 1.59	9.82 ± 1.690	47.75 ± 4.588	1.86 ± 0.371
	S.D.	34.73	1.359	4.50	5.345	14.511	1.174
	Range	232–338	6.12–10.40	20.8–34.3	4.86–21.8	27.38–83.10	0.50–3.86
	n	10	10	8	10	10	10
2-hr ¼ scaled	Mean ± S.E.	241.51 ± 12.53	10.0 ± 0.35	36.7 ± 1.23	10.2 ± 4.23	103.2 ± 8.29	3.08 ± 0.709
	S.D.	34.46	1.01	3.48	11.97	23.4	2.007
	Range	194–314	8.59–11.60	31.0–41.0	0.65–37.30	71.86–138.8	0.98–6.00
	n	8	8	8	8	8	8
4-hr ¼ scaled	Mean ± S.E.	252 ± 18.05	9.80 ± 0.178	37.6 ± 1.66	22.2 ± 9.13	131.0 ± 12.11	2.84 ± 0.600
	S.D.	54.17	0.535	5.00	27.39	36.25	1.699
	Range	161–320	8.82–10.60	27.3–43.6	2.63–87.8	81.43–201.3	0.29–5.03
	n	9		9	9	9	8
28-hr ¼ scaled	Mean ± S.E.	316 ± 13.57	9.40 ± 0.233	38.2 ± 1.07	11.7 ± 3.85	194.6 ± 45.19	1.48 ± 0.376
	S.D.	38.39	0.661	3.04	10.90	127.82	1.065
	Range	264–369	8.54–10.30	32.5–43.5	1.65–36.20	71.20–466.5	0.09–2.82
	n	8	8	8	8	8	8
52-hr ¼ scaled	Mean ± S.E.	281.1 ± 16.01	9.02 ± 0.208	33.8 ± 1.88	4.26 ± 1.01	191.0 ± 33.03	1.50 ± 0.527
	S.D.	45.28	0.588	5.32	2.854	93.43	1.396
	Range	226–354	7.84–9.63	26.1–38.5	0–7.75	67.67–368.3	0.06–3.97
	n	8	8	8	8	8	7

TABLE III. Average body weights, hemoglobins, blood lactate, and blood glucose for deslimed and control rainbow trout, *Salmo gairdneri* (1963).

Conditions		Body weights (g)	Hemoglobin (g/100 ml)	Blood lactate (mg/100 ml)	Blood glucose (mg/100 ml)
Air-dipped controls	Mean ± S.E.	345.1 ± 18.82	10.8 ± 0.33	5.61 ± 0.737	77.43 ± 5.310
	S.D.	59.53	1.05	2.333	16.791
	Range	266–458	9.4–12.4	2.56–11.10	56.39–102.10
	n	10	10	10	10
2–4 hr unscaled controls	Mean ± S.E.	351.8 ± 25.39	12.9 ± 0.48	7.37 ± 1.090	76.54 ± 3.577
	S.D.	71.82	1.38	3.085	10.119
	Range	271–472	11.4–14.8	4.22–11.80	63.70–90.47
	n	8	8	9	8
4–hr deslimed (rock salt)	Mean ± S.E.	318.5 ± 19.98	11.7 ± 0.22	4.95 ± 0.760	87.35 ± 8.601
	S.D.	56.52	0.62	2.152	24.328
	Range	205–388	10.6–12.7	2.15–8.09	38.55–115.10
	n	8	8	8	8
4–hr deslimed (mechanical)	Mean ± S.E.	311.0 ± 16.69	11.8 ± 0.16	5.32 ± 0.710	83.19 ± 4.853
	S.D.	55.37	0.54	2.355	16.095
	Range	233–446	10.8–12.8	2.80–9.29	59.39–118.8
	n	11	11	11	11

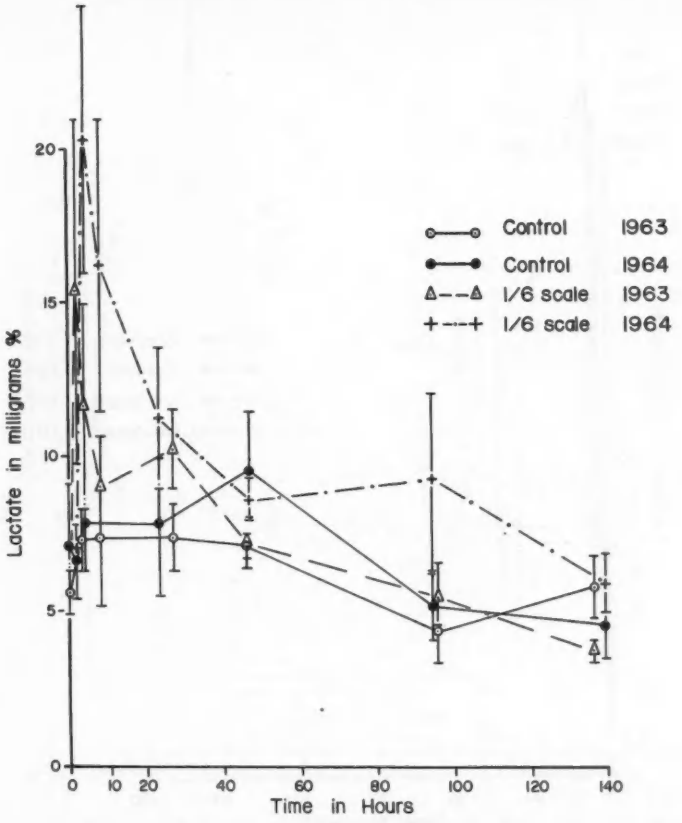

FIG. 4. Changes in blood lactate in 18-month-old rainbow trout (*Salmo gairdneri*) after removal of $\frac{1}{6}$th of body scales and recovery.

to changes induced by mild exercise (Black, 1957a). The tremendous variability both in control and scaled fish may be an expression of the occasional struggling of the fish in the covered hatchery basket.

In Fig. 5, blood lactate data for 1963 and 1964 for $\frac{1}{4}$-scaled fish are illustrated. There was a significant increase ($p < 0.05$) in blood lactate at the 2nd hr after scaling for 1963 data and at the 4th hr after scaling for 1964 data despite marked variability in the control data. As in the $\frac{1}{6}$th-scaled fish, there was a significant increase in blood lactate reflecting a probable increase in activity as a result of the scaling injury.

GLUCOSE

Blood glucose results for experiments carried out on $\frac{1}{6}$th-scaled fish in 1963 and 1964 are illustrated in Fig. 6, and for $\frac{1}{4}$-scaled fish in Fig. 7. The

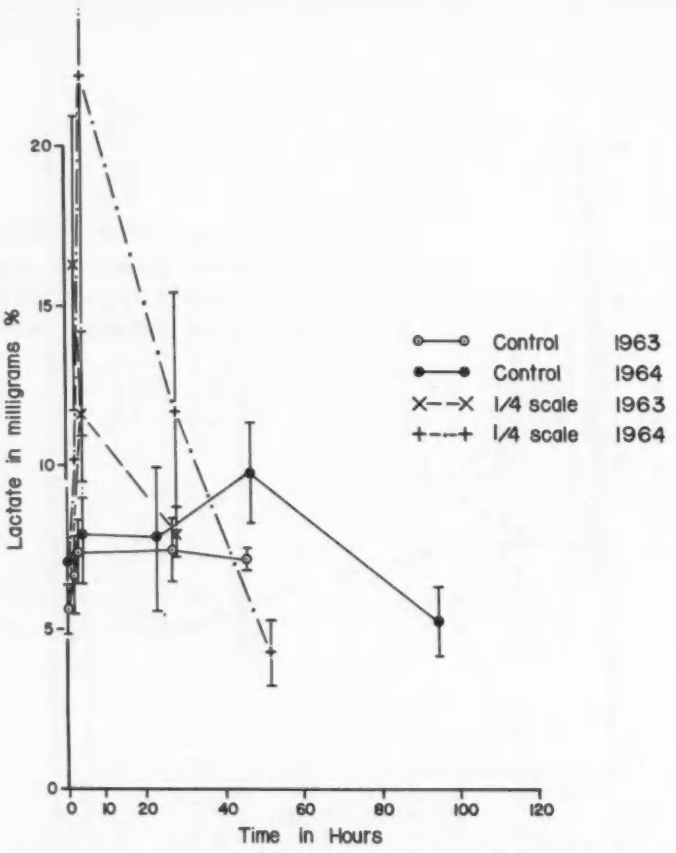

FIG. 5. Changes in blood lactate in 18-month-old rainbow trout (*Salmo gairdneri*) after removal of $\frac{1}{4}$ of body scales and recovery.

increase in blood glucose over the first 36 hr is three- to fourfold. The levels decreased steadily to return to initial values for $\frac{1}{6}$th-scaled fish sometime between 96 and 140 hr after scaling. The $\frac{1}{4}$-scaled experiments were terminated before the full curve was described.

LIVER GLYCOGEN

The course in change in liver glycogen for $\frac{1}{6}$th- and $\frac{1}{4}$-scaled fish is shown for the year 1964 in Fig. 8. During the first 48 hr, control liver glycogen values decreased steadily to one-half the initial value. By the end of 140 hr, liver glycogen was about one-third of the initial value in control fish. In fish that had been scaled, the liver glycogen decreased very rapidly. By the 10th hr, the liver glycogen value for $\frac{1}{6}$th-scaled fish was less than one-half the control

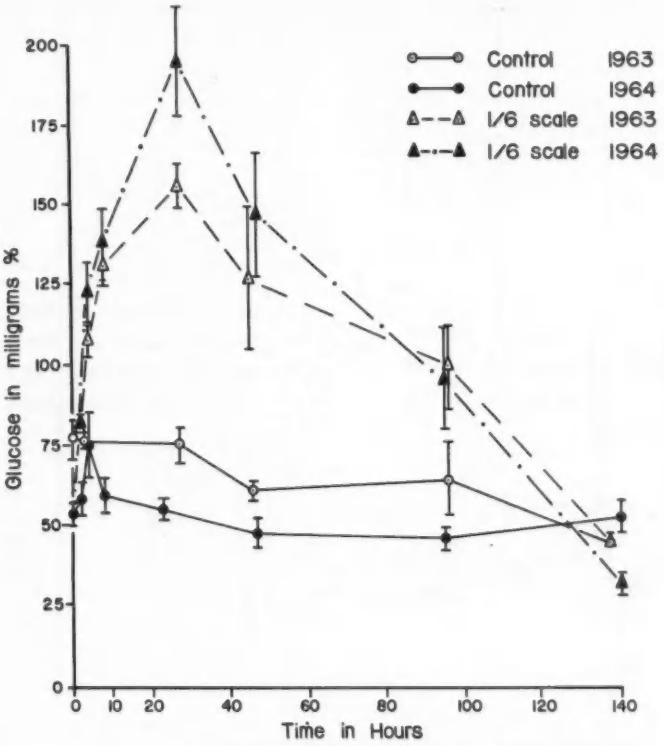

FIG. 6. Changes in blood glucose in 18-month-old rainbow trout (*Salmo gairdneri*) after removal of $\frac{1}{6}$th of body scales and recovery.

value. As shown in Fig. 8, starvation was probably the principal cause of the depletion of liver glycogen; however, the rate and degree of depletion was greater for the scaled fish. The data for the $\frac{1}{4}$-scaled fish are incomplete.

GENERAL DISCUSSION

The hemoglobin levels appeared to increase and then diminish with the time of holding, both in the test fish and the controls (Fig. 1, 2). Changes are very similar to those reported by Black (1957b) for lake trout, *Salvelinus namaycush*, and in rainbow trout, *Salmo gairdneri*, by Black et al. (1962). On the other hand, there was a change in the opposite direction observed in wild stock rainbow trout (Black et al., 1960). Changes in the blood levels of hemoglobin appear to be related as much to the increased lactate concentration induced by confined captivity. At any rate there was some increase in blood lactate during holding (Fig. 4, 5).

Hematocrit levels exhibited changes similar to the hemoglobin levels (Fig. 3).

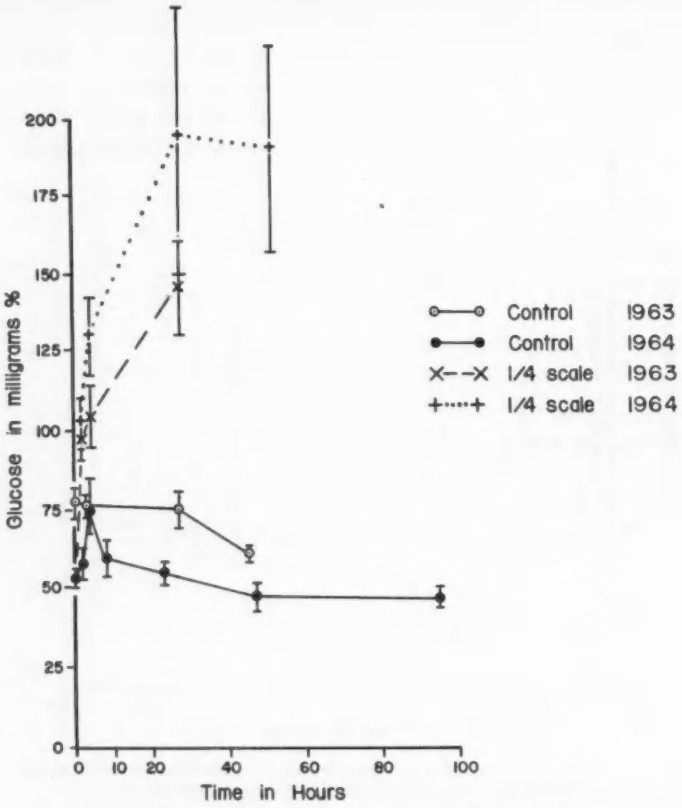

FIG. 7. Changes in blood glucose in 18-month-old rainbow trout (*Salmo gairdneri*) after removal of ¼ of body scales and recovery.

From the above data on hemoglobin levels and hematocrits, a conclusion is reached that the small osmotic shifts are related to activity per se rather than to any shift of water through the scaled surface.

The lactate blood levels did not rise to a value greater than 20 mg/100 ml blood, for either ⅙th- or ¼-scaled trout. However, an average value of 15.4 mg/100 ml in 1963, and 20.3 mg/100 ml in 1964 for ⅙th-scaled fish, and 16.3 mg/100 ml for ¼-scaled trout in 1963 were recorded from fish that had been held for a period of 2–4 hr. This lactate level is seen in 1.5-year-old rainbow trout that had been vigorously exercised for 2 min (Black et al., 1962). A conclusion is reached from the above data that scaling is associated with increased activity which is, in turn, reflected by increased lactate levels. No direct observations were made on activity.

The average blood glucose levels in control fish varied from 47 to 75 mg/100 ml blood both in 1963 and 1964. The average value for rainbow trout in a

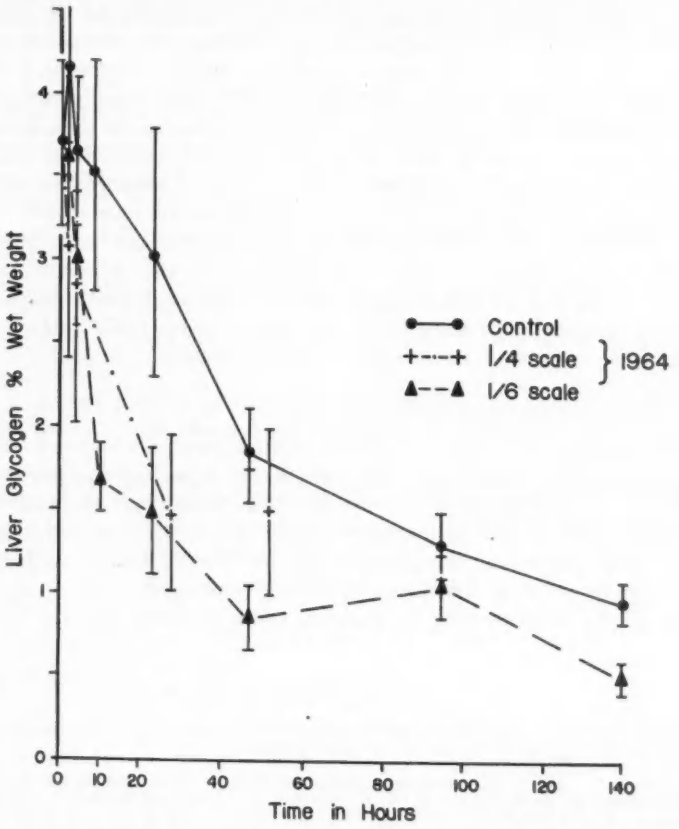

FIG. 8. Changes in liver glycogen in 18-month-old rainbow trout (*Salmo gairdneri*) after removal of $\frac{1}{6}$th and $\frac{1}{4}$ of body scales and recovery.

previous study by Black et al. (1960) was 68.76 mg/100 ml blood. The effect of scaling is to invoke a three- to fourfold rise in blood glucose both in the $\frac{1}{6}$th- and $\frac{1}{4}$-scaled fish (Fig. 6, 7). Blood glucose in deslimed fish had doubled by the end of 4 hr. According to Falkmer (1961), blood glucose in *Cottus scorpius* does not change in starvation for periods up to 5 weeks. Falkmer's findings are confirmed by the control values displayed in Fig. 6 and 7. Hyperglycemia is a common response in man to a variety of pathological conditions including trauma, shock, and infections (Peters and Van Slyke, 1946).

The very high blood sugar level reported by several workers in Kiermeir's (1939) comprehensive study on blood glucose in fishes may have been due to injury.

One source for blood glucose during starvation is the glycolysis of liver glycogen. Liver glycogen levels in the scaled fish were reduced during the

holding period. Glucose could also be mobilised from body fat and/or protein.

In experiments conducted on sockeye salmon, *Oncorhynchus nerka*, in salt water by Black (1957c), death in salmon followed vigorous activity. It was noted that some scaling occurred during these experiments. Without substantiating the point, Black contended that death was due primarily to increased concentrations of lactic acid and not as a result of scaling. In this paper, only one mortality occurred in 175 test fish. There was no evidence of osmotic shifts of water in either partially scaled or deslimed trout. The conclusion is reached, that partial scaling or desliming does not cause death in the first 140 hr subsequent to scaling or desliming. It should be pointed out, however, that death has not occurred as a result of exercise in any of the salmonids studied at Summerland (Black 1957a, b, c; Black et al., 1960, 1962).

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Purines in the Integument of the Atlantic Salmon (*Salmo salar*) During Parr–Smolt Transformation[1,2]

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ABSTRACT

During the parr–smolt transformation in Atlantic salmon, silvery materials were found beneath the scales (scale layer) and deep in the dermis adjacent to the muscle (skin layer). Both layers were thicker in smolts than in parr and both layers contained guanine and lesser amounts of hypoxanthine.

Changes in levels of guanine, hypoxanthine, and the ratio between them (G/H) were measured from late December to late May on 2-year-old parr held in the laboratory under natural photoperiods and at temperatures varying from 6.0 in December to 9.5 C in late May. The change from parr to silvery parr during February and March accompanied sharp increases in guanine, hypoxanthine, and G/H values in the skin layer with less marked increases in the scale layer. The change from silvery parr to smolts during April and May accompanied sharp increases in guanine, hypoxanthine, and G/H values in the scale layer but no change occurred in the trend already established in the skin layer.

Parr held all winter under stream conditions and examined in early April possessed purine levels and G/H ratios in the skin and scale layers comparable to those in laboratory fish during the previous December.

Silvery parr captured migrating seaward in early June had purine levels and G/H ratios in the scale layer similar to those in laboratory smolts in late May but skin guanine values were much lower and the G/H ratio in the skin was extremely low.

INTRODUCTION

Investigations on several species of fish suggest that the whiteness or silveriness is due to amorphous or crystalline purines located in guanophores or iridocytes of the integument. Peschen (1939) extracted guanine from the skin and scales of the bleak (*Alburnus lucidus*); Sumner (1944) measured the amount of guanine in the skin of *Girella nigricans*, while Robertson (1948) observed increased guanine content on the scales of *Salmo gairdneri* during parr–smolt transformation (smoltification). However, guanine is not necessarily the only purine present. Ziegler-Gunder (1956) found appreciable quantities of hypoxanthine as well as guanine in *Alburnus lucidus* and, since the present work commenced, Markert and Vanstone (1966) demonstrated the presence of guanine and hypoxanthine in the belly skin of presmolts, smolts, and grilse of the coho salmon (*Oncorhynchus kisutch*).

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Although the process of integumentary silvering is the most evident feature of smoltification it remains uninvestigated in the Atlantic salmon. The present objectives were to determine the sites of dermal silvering, the nature of the silvery materials, and their quantitative changes during the smoltification of young Atlantic salmon.

MATERIALS AND METHODS

Fish Maintenance

Two-year-old Atlantic salmon, obtained from the Miramichi Fish Culture Station, South Esk, N.B., were held in running aerated fresh water in grey wooden tanks and fed homogenised liver daily. Mean daily water temperatures varied from 6.0 to 9.5 C between December and May. The incandescent illumination above the tanks was regulated by a photocell to correspond to that outside (8 hr in late December to 14 hr in late May). No attempt was made to reproduce natural intensities, wavelengths, or incidences of the light.

Histological Methods

Fish were killed by a blow on the head and pieces of integument (1 cm^2) were removed from the ventral region and fixed in 10% formalin for 1 hr. Sections were cut at 10–15 μ and stained in Erhlich's hemotoxylin and eosin. Slides were studied using reflected or transmitted light.

Qualitative Methods

Scales and skin were removed and suspended in neutral, alkaline, or acidic extraction solutions (Table I). In each solution the tissues were agitated for approximately 10 min with a magnetic stirrer to facilitate the extraction of the compounds.

A volume (0.1–0.9 ml) of the extract was spotted with a 1-ml volumetric pipette on Whatman No. 3 or No. 1 filter paper and dried in a current of air. Five to 100 μl of 4 mM solutions of guanine, hypoxanthine, adenine, xanthine, uric acid, adenosine, guanosine, and guanosine monophosphate (GMP) (Sigma Chemical Co., Sigma grade) and adenosine triphosphate (ATP) Nutrional Biochemicals Corp.) were spotted as standards.

Chromatograms were run in several descending solvent systems (Table I). Compounds were located by absorbance and fluorescence under ultraviolet radiation (Mineralamp UVS.11, 253.57 mμ) and tentatively identified by comparing their Rf values with those of standards. The sample and standard spots, each with a reference blank (an area equal in size and corresponding to the same Rf as the sample or standard involved), were cut from the chromatograms and separately eluted in test tubes for 12 hr in 3–8 ml of either 0.1 N HCl or 0.1 N NaOH. At the start and finish of the 12-hr elution the tubes were agitated and following agitation the pieces of filter paper removed. The remaining solution was centrifuged at 1800 g for 10–15 min to remove

TABLE I. *Rf* values for skin extracts and standard compounds separated by descending chromatography in several solvent systems.

Extraction solvent:	Distilled water	0.5 N NaOH	10% NH_4OH	3 N NH_4OH	1 N HCl	1 N HCl	1 N HCl
Chromatographic solvent:	Water *p*H 10	5% Na_2HPO_4 sat'd with isoamyl alcohol	Water *p*H 10	Butanol–acetic acid–H_2O (4:1:1 v/v)	Isopropanol–HCl–H_2O (170:41:39 v/v)	Butanol–acetic acid–H_2O(4:1:1 v/v)	Methanol–HCl–H_2O (70:20:10 v/v)
Skin extract	0.38, 0.60, 0.88	0.45, 0.56	0.42, 0.67 0.87	0.05, 0.13 0.23, 0.33	0.15, 0.23	0.06, 0.10 0.24, 0.35	0.20, 0.33 0.45
Standard compounds							
Guanine	0.42	0.45	0.42	0.23	0.15	0.23	0.20
Hypoxanthine	0.67	0.56	0.67	0.33	0.22	0.33	0.33
Adenine	0.40	0.40	0.41	0.48	0.25	0.48	0.34
Xanthine	0.70	0.50	0.70	0.24	0.20	0.24	0.29
Uric acid	–	0.41	–	–	–	–	–
Guanosine	0.68	–	0.68	0.15	–	0.15	–
Adenosine	0.55	–	0.55	0.31	–	0.31	–
ATP	0.98	–	0.98	0.00	–	0.00	–
GMP	0.95	–	0.95	0.02	–	0.02	–

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Adenosine	0.55	–	0.55	0.31	–	0.31	–
ATP	0.98	–	0.98	0.00	–	0.00	–
GMP	0.95	–	0.95	0.02	–	0.02	–

paper fibers. The supernate was poured carefully into clean tubes and aliquots analysed against their appropriate blanks on a Beckman DK-1A ratio recording spectrophotometer between 320 and 220 mμ.

Quantitative Methods

Before each analysis 10 fish were selected randomly, starved for 3 days, and then sampled over a 2-day period. Each fish was classified by visual observation as a parr (parr marks, no silver and yellowish flanks and fins), a silvery parr (parr marks and incomplete silvering), or a smolt (no parr marks and silver). They were then killed, weighed, and the fork length measured.

The scale and skin silvery layers were treated separately. To extract the silvery scale layers from beneath the scales it was necessary to remove the epidermis, the scales, and silvery materials and a small portion of the dermis from a designated area occupying almost the entire lateral half of the fish. This was accomplished by bringing a sharp straight-edged scalpel against the dermal tissues. Following removal, the skin was scraped lightly. The fish was then frozen for approximately 1 hr. When firmly frozen an incision was made around the scraped area and the remaining skin lifted from the body musculature. Any silvery materials still adhering to the muscle were scraped off with the scalpel and added to the skin extract. By this procedure a negligible amount of muscle was removed. The scales were placed in 4 ml 1 N HCl in a stendor dish, covered, agitated for 10–15 min by a magnetic stirrer, and then allowed to stand for 4–5 hr. The skin was treated in the same manner but without agitation. Subsequent treatments were identical for skin and scales.

After extraction the tissue and solvent were poured from the stendor dishes into centrifuge tubes. The stendor dishes were washed twice with 1 ml 1 N HCl and the washings added to the centrifuge tubes. The residual tissues were spun down at 1800 *g* and the supernate poured off. The tissues were resuspended and centrifuged three times in 1 ml 1 N HCl. The supernate and the three washes were added to a graduated cylinder and their total volume read. Following purine extraction, the tissues were transferred to tared weighing bottles, dried for 12 hr at 107 C, placed in a desiccator for 1–2 hr, reweighed, and the dry weight of tissue calculated.

Chromatograms were run on Whatman No. 1 filter paper, descending, in methanol–HCl–water (70:20:10 v/v) (Kirby, 1955). Guanine and hypoxanthine spots and blanks were eluted with 0.1 N HCl for 12 hr and aliquots analysed spectrophotometrically. The concentration of guanine or hypoxanthine in each extract was determined by substituting the absorbance value at 248 mμ in the following equation:

$$\text{Concentration (moles/liter)} = \frac{\text{Absorbance}}{\text{Molar extinction coefficient}}$$

where the extinction coefficient at 248 mμ and *p*H 1 was 11,400 for guanine and 10,800 for hypoxanthine (Johnson et al., 1955). The product of the molecular weight, the elution volume, and the total extract volume divided by

the spot volume gave the weight of purine (guanine or hypoxanthine) in an extract. The purine bases extracted were expressed as percentages of the dry weight of the tissue and purines:

$$\text{Per cent purine extracted} = \frac{\text{Purine } (mg) \times 100}{\text{Dry tissue} + \text{guanine} + \text{hypoxanthine } (mg)}$$

RESULTS

Location of Silvering in the Integument

Two distinct layers of silvering were observed in the integument of smolts (Fig. 1). The outer layer was directly beneath the scales while a deeper layer, probably corresponding to the stratum argenteum described by Cunningham and MacMunn (1893), was immediately above the muscle. Both layers appeared to contain needle-like crystals. These layers correspond to the crystalline layers described by Denton and Nicol (1965) for *Alburnus alburnus*.

Both layers were present in parr also but were not as thick as those in smolts.

Qualitative Analysis

Compounds were identified by comparing the R*f* values of sample spots and their absorption spectra with those of known purines, nucleosides, and nucleotides. Table I represents the R*f* values obtained for both sample and standard compounds in acidic, neutral, and basic extraction and chromatographic solvents. Figure 2 represents the ultraviolet absorption spectra for extract and standard solutions of guanine and hypoxanthine in 0.1 N HCl.

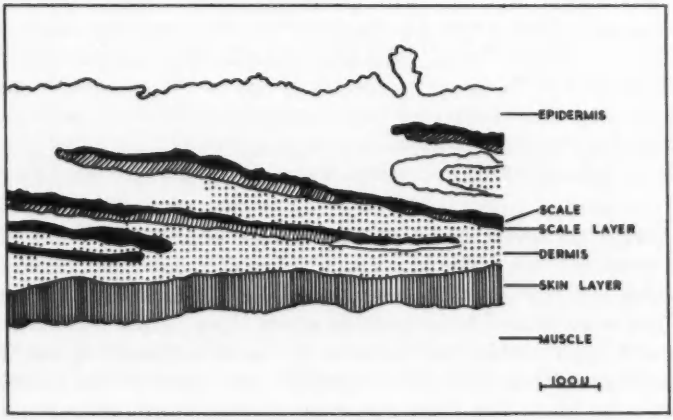

FIG. 1. A camera-lucida drawing of the integument of an Atlantic salmon smolt showing the scale and skin silvery layers.

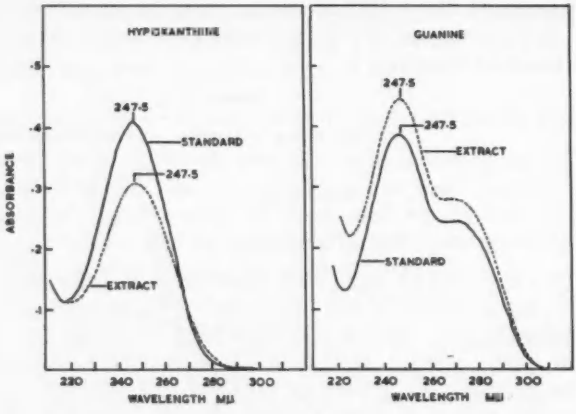

FIG. 2. Ultraviolet absorption spectra for extract and standard solutions of guanine and hypoxanthine in 0.1 N HCl.

In an acidic system purines are more soluble than in neutral or alkaline systems, but under acid conditions degradation of nucleosides, nucleotides, and oligo-nucleotides to the constituent bases can occur. In alkaline media this hydrolysis does not take place, but hydrolysis does occur at the phosphate-ester linkage to produce nucleosides. In neutral systems neither of the above hydrolyses occur. Consequently, a variety of acid, basic, and neutral extraction and chromatographic solvent systems were used to determine what purines are present and whether they are free purines in the tissues or incorporated into nucleosides or nucleotide structures.

On the basis of R*f* values and individual spectra, only guanine and hypoxanthine were detected in all systems. No other purines, nucleosides, or nucleotides were found. Spots, other than guanine and hypoxanthine, did not correspond with the R*f* values or spectra of any of the standard compounds. Their violet and blue florescence under ultraviolet (360 mμ) suggested that they might be pterines. Individual pterines were not identified since they probably contribute little to silvering (Hama, 1963; Stackhouse, 1966).

Quantitative Analysis of Guanine and Hypoxanthine During Smoltification

At intervals of 3 weeks between late December and late May, samples of 8–10 fish were removed from the laboratory population and the levels of guanine and hypoxanthine measured in the skin and scale layers (Fig. 3). In the scale layer the majority of the guanine and hypoxanthine was deposited from March to May. The March increase coincided with an increase in the number of smolts in each sample. Guanine values were always higher than the hypoxanthine values. Increases in guanine were accompanied by increases

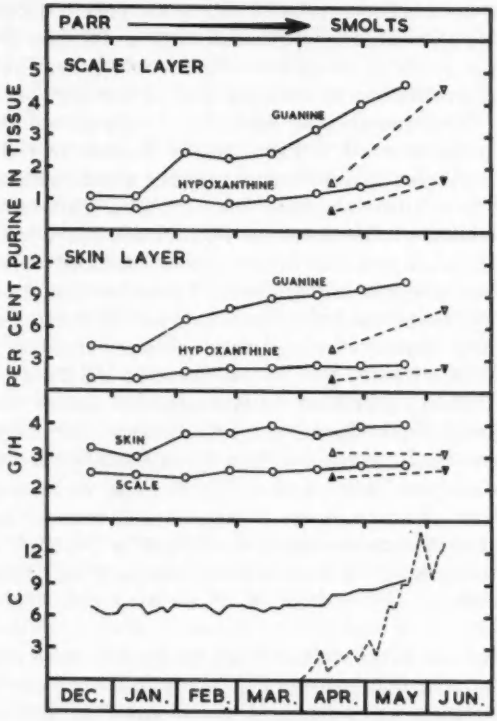

FIG. 3. Seasonal changes in guanine, hypoxanthine, and G/H levels in the scale and skin silvery layers for laboratory fish, fish from the Miramichi Fish Culture Station (guanine △, hypoxanthine ▲), and migrating stream fish (guanine ▽, hypoxanthine ▼). Each point represents the mean of 8–10 determinations. Water temperature at laboratory (————); at Curventon and at South Esk (– – – – –).

in hypoxanthine but the guanine to hypoxanthine ratio (G/H) increased significantly between December and April ($t = 2.66$, df $= 18$, $P < .05$).

In the skin layer, guanine and hypoxanthine values rose sharply between January and February and then increased steadily until early June. Unlike the scale layer there was no sharp increase at smoltification. The early February rise coincided with the change from parr to silvery parr. A significant rise ($t = 2.36$, df $= 17$, $P < .05$) in the G/H of the skin layer occurred between January and February, after which time no significant change was recorded. The guanine and hypoxanthine values and the G/H ratio were always much greater in the skin layer than the scale layer.

The data for the laboratory population suggest that the transition from parr to silvery parr correlates with skin purine deposition while the transition

from silvery parr to smolts correlates with scale purine deposition. Furthermore, increases in purine deposition coincide with an increase in the G/H ratio.

In view of the artificial conditions which could prevail in the laboratory it was considered worthwhile to compare the laboratory fish with fish maintained outdoors. Consequently, on April 15, 10 2-year-old parr were transported alive from the Miramichi Fish Culture Station to the laboratory. At South Esk they had been maintained in outdoor ponds which, like the river, were frozen over from late November to early April. Laboratory fish in April were turning into smolts while these fish from South Esk were classed as parr. Purine levels in the scale and skin layers of these outdoor fish corresponded to those obtained from the laboratory fish in December and January and were approximately 50% lower than the laboratory fish in April. Furthermore, the G/H ratios for both layers were significantly lower than for the laboratory fish in April ($t = 5.64$, df = 16, $P < .01$; skin layer, $t = 3.28$, df = 14, $P < .05$).

On June 8, 10 silvery parr from the downstream "smolt" run were captured at the counting fence at Curventon, Northwest Miramichi. They were transported alive to the laboratory and analysed the following day. The purine values for the scale layer were comparable to those of laboratory smolts in mid-May. However, the skin layer of migrants contained significantly less guanine than that of laboratory fish ($t = 6.57$, df = 16, $P < .01$). The G/H ratio was significantly lower in both layers in the migrants than it was in the laboratory fish (skin, $t = 6.54$, df = 16, $P < .01$; scales, $t = 3.23$, df = 17, $P < .01$).

Assuming that the fish obtained from South Esk were representative of stream fish then a more rapid purine deposition takes place in nature than in the laboratory although it commences much later. In nature the increase occurs in both scale and skin layers together, but to a lesser degree in the skin layer. The G/H ratio is lower under stream conditions and unlike the laboratory fish it does not increase greatly during smoltification.

DISCUSSION

This study of silvering during smoltification of Atlantic salmon poses two interrelated questions. What environmental factors are controlling the increase in purine deposition and what are the underlying changes in purine metabolism?

Environmental Factors

The most marked difference in environment between laboratory and stream fish was water temperature. The laboratory fish were held at 6–7 C until early April followed by a steady increase to 9.5 C in late May. Stream fish were subjected to temperatures as low as 0 C from late December to late March but then experienced a rapid increase to 13 C in late May. The higher overall mean temperature of the laboratory fish and their higher metabolic rates could be responsible for their considerably advanced purine deposition. Furthermore, the more rapid purine deposition in the scale layer of stream

populations correlates with the rapid rise of stream temperatures. However, controlled experiments are necessary to establish a causal relationship between temperature and purine deposition.

Temperature could exert its effect through influence on feeding activity, since it is generally recognized that Atlantic salmon do not feed appreciably at temperatures below 4 C. While stream fish at temperatures as low as 0 C probably subsisted on body reserves from late December to April, laboratory fish under warmer conditions were fed a high protein diet daily. Since purines are probably derived from amino acids this substantial dietary protein could lead to increased purine deposition.

Where light is concerned both photoperiod and intensity should be considered. While it is probable that a lengthening spring photoperiod may prime the parr in some way, the differences in time of onset of silvering between laboratory and stream fish exposed to comparable photoperiod regimes suggest that photoperiod is not the sole controlling variable. This idea is supported by Van Overbeeke who found that although a short photoperiod could inhibit silvering in coho salmon it could not suppress it entirely (Hoar, 1965).

The intensity of incident light to which the laboratory fish were exposed was low (< 4 ft-c), but they were held on a light grey background. Stream fish during the entire winter were under snow-covered ice and were presumably exposed to extremely dim conditions and a darker background. The shade of the background has been shown by Sumner (1944) to effect the amount of guanine in the skin of *Girella nigricans* and fish held 4 months on a white background had four times more guanine than those held on a black background. Since the purine level in the skin layer of stream fish in April was comparable to the level of the laboratory fish in December it is conceivable that the increase in purines in the skin of laboratory parr in February could be attributed to a lighter shade of their surroundings and not necessarily be associated with smoltification.

Finally, young salmon in their descent to the ocean are subjected to changes in salinity. While the production of completely silver smolts held in the laboratory in fresh water demonstrates that increased salinity is not obligatory for smoltification, it is possible that final silvering of silvery parr in nature could be influenced by it.

It is concluded that temperature, photoperiod, intensity of incident and background illumination, feeding, and increases in salinity could be influencing purine deposition during smoltification. Controlled experiments are now in progress to test the influence of these variables.

Purine Metabolism

It is generally recognized that purines are synthesized through the *de novo* pathway of nucleotide synthesis which first involves the formation of inosinic acid. Inosinic acid is converted through a series of reactions to form the free purine bases. In biological systems there is no evidence for synthesis *de novo* of free purines.

Svard (1958) estimated the acid-soluble nucleotides in the blood of Atlantic salmon parr and smolts. He found that inosine monophosphate was low and that guanosine triphosphate was high in the pre-metamorphosis period while at the time of metamorphosis inosine monophosphate was high and guanosine triphosphate was low. This suggests that the deposition of guanine in the integument may arise from nucleotide catabolism. Investigations of the changes in purine metabolism at parr–smolt transformation are now being carried out.

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Pyloric Caeca and Gill Raker Development in Lake Trout, *Salvelinus namaycush*, in Algonquin Park, Ontario[1,2]

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Maple, Ontario

ABSTRACT

Counts of pyloric caeca and gill rakers were made on lake trout (*Salvelinus namaycush*) in three Algonquin Park lakes where the trout were dependent on plankton for food in varying degrees. In 798 trout from the three lakes, pyloric caeca counts ranged from 105 to 210 and varied with the size of trout. There was no association between numbers of caeca and type of food eaten.

Gill raker counts were made on 930 lake trout. Numbers of rakers are not related to size or sex of lake trout in the sample. Gill raker counts ranged from 17 to 26 in the combined populations. An association exists between the numbers of gill rakers, their length, and the amount of plankton eaten by the lake trout. Accessory gill rakers on the medial surface of the gill arch are described. The number and development of these rakers were associated with the amount of plankton eaten by the lake trout.

INTRODUCTION

Studies are currently being carried out in Algonquin Park, Ont. lakes on the significance of food habits in the general biology of the lake trout (*Salvelinus namaycush*). Certain aspects of this investigation, including the effects of diet on rate of growth, longevity, size, and age at maturity of lake trout have been reported by Martin (1966). The present study investigates whether any association exists between diet and lake trout morphology, specifically with reference to the development of pyloric caeca and gill rakers.

In the various lakes of Algonquin Park the lake trout may become largely piscivorous or planktonivorous in the summer months depending on the availability of suitable forage fish at this time. It has been shown, notably by Russian workers (Svetovidov, 1934; Reshnetnikov, 1961; Savvaitova, 1962) that a correlation exists between food habits and fish morphology. These authors state the numbers of gill rakers and pyloric caeca are adapted to the type of food eaten.

Lake trout in three Algonquin Park lakes, Louisa, Happy Isle, and Opeongo, were used for the present study. In these lakes plankton occurred, respectively, in 64.0, 55.6, and 0.9% of the lake trout stomachs in the period mid-June to mid-September (the approximate period of thermal stratification). The remaining stomachs contained chiefly various forage fish, immature aquatic stages of insects, or were empty.

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Fork length has been used in this study since many of the samples were obtained through the creel census where this measurement is used. In approximately 60% of the lake trout sampled, total, fork, and standard length measurements were made in the metric system. Table I presents length conversion data for the three lake trout populations under study.

TABLE I. Conversion factors for total, fork, and standard lengths for lake trout in Louisa, Happy Isle, and Opeongo lakes.

Lake	Total	Fork	Standard	N
Total				
Louisa	–	0.90240	0.81727	236
Happy Isle	–	0.89672	0.82031	123
Opeongo	–	0.90859	0.82560	144
Mean:	–	0.90281	0.82087	
Fork				
Louisa	1.10816	–	0.90566	–
Happy Isle	1.11517	–	0.91478	–
Opeongo	1.10060	–	0.90865	–
Mean:	1.10765	–	0.90924	
Standard				
Louisa	1.22359	1.10416	–	–
Happy Isle	1.21906	1.09316	–	–
Opeongo	1.21124	1.10053	–	–
Mean:	1.21822	1.09982	–	–

PYLORIC CAECA

Figure 1 shows mean pyloric caeca counts for 798 lake trout from Louisa, Happy Isle, and Opeongo lakes collected during 1963, 1964, and 1965. Numbers of caeca are extremely variable in these lake trout ranging from 105 to 210 in Lake Louisa, 102 to 192 in Happy Isle Lake, and 111 to 190 in Lake Opeongo. The number of caeca bear a relationship to the size of trout and the three populations showed a generally similar pattern in their development. Characteristically there is a rapid increase in numbers in fish up to length of about 25–30 cm followed by a levelling-off phase in larger lake trout. No consistent differences were observed in counts in male and female lake trout in the same size ranges.

Analysis of variance using the method of fitting constants (Snedecor, 1959) was carried out for fish 25 cm and over in length for the three lakes for

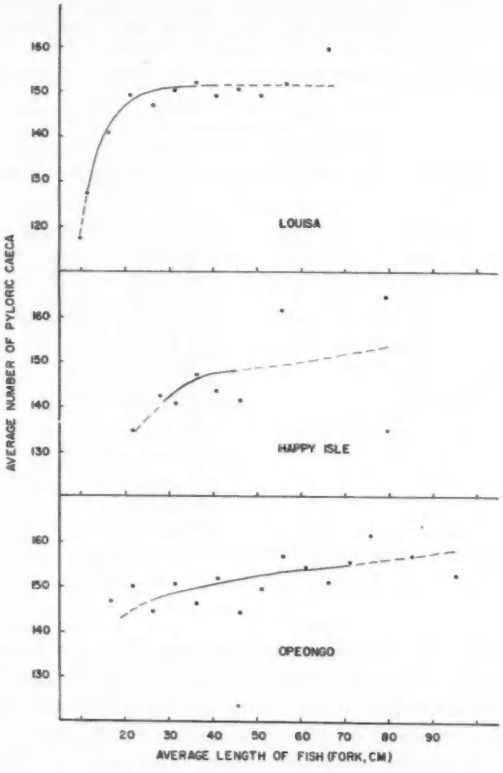

FIG. 1. Average numbers of pyloric caeca in 5-cm length-groups of lake trout from Louisa, Happy Isle, and Opeongo lakes. Broken lines indicate samples of less than five fish.

the years 1963 through 1965 (Table II). This method was required because of the non-orthogonality of the sampling. Interaction was not significant. No significant differences were found in the caeca counts between years but highly significant differences existed in counts between lakes. The pyloric caeca values for Happy Isle Lake (144.1) were appreciably lower than those in Lake Louisa (151.5) and Lake Opeongo (151.1).

GILL RAKERS

Gill raker counts and measurements were made on 930 lake trout from the three study lakes (Table III). All counts were made on the first arch on the left side of the fish and all rudimentary rakers were included.

No consistent trends were apparent in the numbers of gill rakers as related to the size or the sex of the trout. Analysis of variance, again using the method

TABLE II. Analysis of variance for pyloric caeca counts in lake trout 25 cm and over (fork length) in Louisa, Happy Isle, and Opeongo lakes for the years 1963, 1964, and 1965. Analysis by method of fitting constants (Snedecor, 1959).

		1963	1964	1965	
Lake	Constants:	$a_1 = -0.27861$	$a_2 = -1.23942$	$a_3 = 1.51808$	Mean
Louisa	$b_1 = 2.61842$	151.27101	150.31020	153.06770	151.54602
Happy Isle	$b_2 = -4.79028$	143.86231	142.90150	145.65900	144.14092
Opeongo	$b_3 = 2.17546$	150.82805	149.86724	152.62474	151.10666
Mean:		148.65379	147.69298	150.45048	

Source of variation	Degrees of freedom	Mean square
Lakes	2	2430.95**
Years	2	138.29(ns)
Interaction	2	0.91(ns)
Individuals	664	211.35

Correction = 5460.71637–5299.59619 = 161.12018.

of fitting constants, was performed on the data from the three lakes for the sampling years 1962, 1963, and 1964 (Table IV). Interaction was not significant. A significant difference in the counts of rakers between years is indicated. This variation is attributed to the enumeration of the rakers rather than to an actual change in numbers between years. The counts for 1964 were made by a different enumerator than those for 1962 and 1963. As the largest samples in each lake are from 1964 and as the difference in counts is generally consistent throughout, a grouping of the data from the 3 years for comparative purposes is felt to be justified. A highly significant difference in the gill raker counts between lakes is indicated in Table IV. Lake Louisa lake trout average about 0.5 a raker more than do the Happy Isle fish and 1.3 more than the Opeongo.

As a further assessment of gill raker development, the length of the largest raker on the first gill arch was measured. Figure 2 shows these data as related to various size-groups of lake trout. Characteristically an initial rapid relative increase in raker length is followed by a relative decrease in their length in the larger fish. Happy Isle values are largely intermediate between those of Louisa and Opeongo. Analysis of covariance was carried out for lake trout in comparable size ranges (22.0–54.9 cm) in the three populations (Table V). This analysis indicates a highly significant difference between the three regression coefficients.

In the course of the examination of the primary gill rakers the presence of a row of accessory gill rakers in the medial surface of the gill arch was noted

TABLE III. Mean number of primary gill rakers on first gill arch for various size-groups of lake trout in Louisa, Happy Isle, and Opeongo lakes. Sample sizes shown in parentheses.

Length-group	Lake		
	Louisa	Happy Isle	Opeongo
(Fork, *cm*)			
5–9.9	23.67 (3)	–	–
10–14.9	22.55 (22)	–	–
15–19.9	22.66 (47)	–	19.00 (2)
20–24.9	22.15 (39)	21.78 (9)	20.38 (16)
25–29.9	22.27 (37)	21.20 (10)	21.38 (45)
30–34.9	21.92 (61)	21.88 (24)	20.95 (86)
35–39.9	22.36 (50)	22.15 (111)	21.19 (77)
40–44.9	21.70 (10)	22.14 (22)	20.80 (50)
45–49.9	21.67 (3)	22.44 (9)	20.98 (41)
50–54.9	19.00 (1)	21.30 (2)	20.50 (47)
55–59.9	–	–	21.15 (20)
60–64.9	–	–	20.97 (29)
65–69.9	23.00 (1)	–	21.35 (34)
70–74.9	–	–	20.92 (13)
75–79.9	–	20.00 (1)	21.00 (5)
80–84.9	–	–	–
85–89.9	–	–	19.50 (2)
90–94.9	–	–	–
95–99.9	–	–	20.00 (1)
Grand mean	22.26	22.05	21.06
Range	18–26	17–25	16–25
N	274	188	468

(Fig. 3). These, to the best of our knowledge, have not been previously described for lake trout.

The accessory rakers are smaller and fewer in number than the primary rakers. As a measure of their degree of development, categories of pointed and nonpointed were established. A nonpointed accessory gill raker is defined as a bony nodule embedded in the dermal covering of the medial surface of the gill arch. The "pointed" category includes all accessory rakers having protuberances either partially imbedded or completely free. In some individuals, one or more of the accessory rakers may be almost as large as the primary gill rakers. Treatment of the gill arch in an alizarin–KO_4 solution (Hollister, 1934) resulted in a similar staining of both primary and accessory gill rakers.

An analysis of variance (Table VI) was performed on the data transformed to $\sqrt{X + 1}$ to determine if there was a significant difference in the mean numbers of accessory gill rakers for the three populations or in the mean

TABLE IV. Analysis of variance for primary gill raker counts in lake trout 25 cm and over (fork length) in Louisa, Happy Isle and Opeongo lakes for the years 1962, 1963, and 1964. Analysis by method of fitting constants (Snedecor, 1959).

		1962	1963	1964	
Lake	Constants:	$a_1 = 0.131991$	$a_2 = 0.154957$	$a_3 = -0.286949$	Mean
Louisa	$b_1 = 0.600017$	22.640822	22.663788	22.221882	22.508831
Happy Isle	$b_2 = 0.148700$	22.189505	22.212471	21.770565	22.057514
Opeongo	$b_3 = -0.748718$	21.292087	21.315053	20.873147	21.160096
Mean		22.040805	22.063771	21.621865	

Source of variation	Degrees of freedom	Mean square
Lakes	2	150.16**
Years	2	19.52**
Interaction	4	1.46(ns)
Individuals	855	2.11

Correction = 379.32896–359.348726 = 19.980234

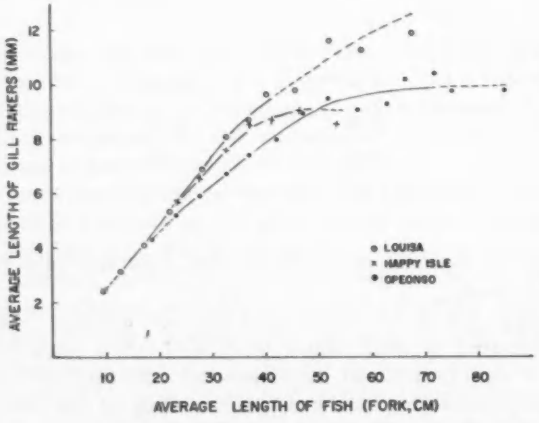

FIG. 2. Average lengths of longest gill raker on first gill arch for various size-groups of lake trout in Louisa, Happy Isle, and Opeongo lakes. Broken lines indicate samples of less than five fish.

proportion of accessory rakers in the pointed condition. Considerable overlap in the range was observed within the three populations, both in the number of accessory gill rakers and in the degree of development as expressed by the proportion of pointed rakers. However, the means in each analysis were found

TABLE V. Analysis of covariance on length of longest gill raker on first gill arch for length of lake trout 22.0–54.9 cm (fork length) (1959–1964).

Lake	df	Σx^2	Σxy	Σy^2	b	df	Deviation from regression: mean square
Louisa	118	3279.9071	72.73583	2.16199	0.02217	117	0.0046
Happy Isle	123	3973.9210	56.28470	1.57537	0.01416	122	0.0064
Opeongo	193	11816.8147	179.42025	3.74967	0.01518	192	0.0053
Within lakes						431	0.0054
Regression coefficient						2	0.0729
Common regression	434	19070.6428	308.44078	7.48703	0.01617	433	0.0058

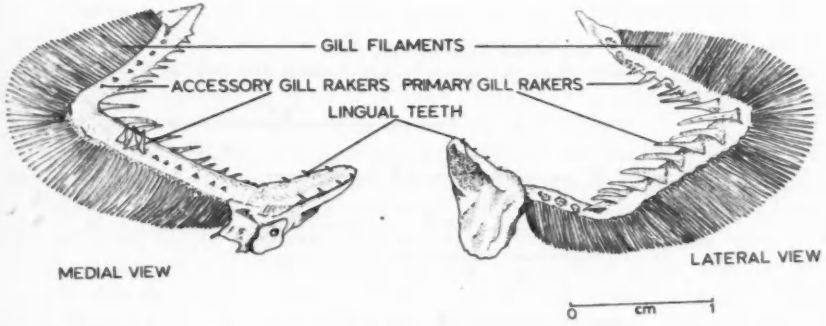

FIG. 3. Two views of left first gill arch of a Louisa Lake trout showing position of accessory gill rakers.

to differ ($p < 0.01$). The standard deviation and standard error of the means were also calculated. The mean ± 2 (standard deviation), the mean ± 2 (standard error), and the range are presented graphically (after Hubbs and Hubbs, 1953) in Fig. 4.

Difference in the degree of development may be shown by the proportion of accessory gill rakers reaching a pointed state. This proportion was derived by dividing the number of pointed accessory gill rakers by the total number of accessory rakers present. The mean proportion value for the Louisa trout was 0.508, that is about one-half of all accessory rakers were pointed. The values for Happy Isle and Opeongo fish were about one-third (0.291) and one-seventh (0.147) respectively.

TABLE VI. Analysis of variance for mean number of accessory gill rakers per arch and mean proportion of accessory gill rakers pointed for three populations of lake trout.

Lake	Mean	Sample size	Number of accessory gill rakers per arch: Range	SD	SE
Louisa	11.2	160	5–16	0.358	0.0283
Happy Isle	7.0	66	0–12	0.466	0.0573
Opeongo	5.5	234	0–16	0.553	0.0361
Analysis of variance:	Variance between means = 45.5 Variance within observations = 0.232; F = 196.2 Level of significance = 0.1%.				
			Proportion of accessory gill rakers pointed		
Louisa	0.508	160	0–0.890	0.0787	0.0062
Happy Isle	0.291	66	0–0.750	0.097	0.0119
Opeongo	0.147	234	0–0.800	0.0812	0.0053
Analysis of variance:	Variance between means = 1.321 Variance within observations = 0.0069; F = 190.8 Level of significance = 0.1%.				

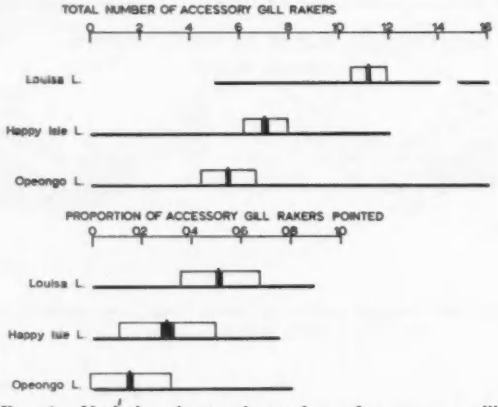

FIG. 4. Variation in total number of accessory gill rakers and degree of development in three lake trout populations.

DISCUSSION

PYLORIC CAECA

In general, numbers of pyloric caeca appear somewhat higher in the three Algonquin Park populations than those reported by others. Vladykov (1954) notes a range of 108–173 caeca with a mean figure of 137.9. Morton and Miller (1954) found a range of 95–170 with a mean value of 126.7. However, as these investigations do not include length data for their lake trout and as it has been shown that numbers of caeca vary with size of trout, no direct comparison can be made with the Algonquin Park data.

The general pattern of caecal development for various sizes of lake trout in the three study lakes is somewhat similar to that observed by Reshnetnikov (1961) for the char *Salvelinus malma* in the Kamchatka River system. Vladykov (1954) has observed an increase in caecal numbers with age in the Sunapee trout, *Salvelinus auroleus*.

Svetovidov (1934), reviewing the literature on pyloric caeca development for a wide range of fish species, found a correlation between numbers of caeca and the character of the food eaten. Reshnetnikov (1961) in a detailed study of Kamchatka char (*Salvelinus malma*) observed a similar correlation in caeca development in three forms of this species which had markedly different food habits. These authors believe that fish eating more hard-to-digest foods require a greater number of pyloric caeca to increase the digestive area. On the basis of the Algonquin Park data this association does not hold for lake trout. The most piscivorous population (Opeongo) had numbers of caeca intermediate between those of the more planktonivorous populations.

Gill Rakers

Gill raker counts for the three Algonquin Park populations show general agreement with those in other areas. Miller and Kennedy (1948), from a sample of 14 lake trout from Great Bear Lake, had counts ranging from 17 to 26 with an average of 23.07. Vladykov (1954), for a sample of 27 lake trout, gives a range of 19–23 rakers with a mean value of 22.0.

The data indicate an association between gill raker development and feeding habits in the three Algonquin Park populations studied. Lake Louisa trout, the most highly planktonivorous (64.0%), had the greatest numbers of and most highly developed primary and accessory gill rakers. Happy Isle trout, which are somewhat less planktonivorous (55.6%), had slightly fewer rakers of both types and they were not quite as well developed. Lake Opeongo lake trout, which are almost entirely piscivorous, average one primary and 1.5–5.5 fewer accessory gill rakers than do the Happy Isle and Louisa trout. The primary gill rakers in the Opeongo trout are about 10% shorter than those in the plankton-feeding fish while the accessory rakers are largely rudimentary in nature. Reshnetnikov (1961) found similar adaptations in the primary rakers of the Kamchatka char.

CONCLUSIONS

An association was found between feeding habits and gill raker development in Algonquin Park lake trout but not with number of pyloric caeca. Although a cause and effect relationship cannot be proven, it is suggested the higher development of gill rakers in the plankton-feeding populations is an adaptation to this type of food.

The great variation in caecal counts and their relationship to size of lake trout emphasize the need of large samples to adequately describe them in any one population.

ACKNOWLEDGMENTS

The assistance of Mrs E. Jermolajev in carrying out counts and translating Russian literature has been appreciated. Miss Pauline Barley assisted in the counting of rakers and caeca. Patient guidance in statistical analysis was provided by J. McFadden and F. A. Raymond. K. H. Loftus and C. C. Lindsey kindly reviewed the manuscript.

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Introduction to Biological Studies of Ogac Lake, a Landlocked Fiord on Baffin Island[1,2]

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ABSTRACT

Ogac Lake is the almost isolated head of a fiord, Ney Harbour, on the south coast of Frobisher Bay, N.W.T. Earlier knowledge of the lake is summarized, a brief account is given of expeditions to the lake in 1957 and 1962, and the scope of the studies is outlined.

EARLIER KNOWLEDGE OF THE LAKE

That large codfish existed in a lake at the head of an inlet of Frobisher Bay had long been known to Eskimos and rumored among white residents and visitors to southern Baffin Island. There is no record of a visit until 1927, when two specimens of cod were collected from the lake by the Rawson–MacMillan expedition of 1927–28 and deposited in the Field Museum of Chicago (Museum No. 30974, 30975). The museum labels imply that the fish were taken from a lake at the head of "Griffin Bay," but apparently no mention is made of them in any scientific report. In 1937, C. H. Ney established a geodetic bench mark on the shore of the inlet which now bears his name, Ney Harbour. Codfish were taken from a lake at the head of this inlet, and the lake appears on later maps as "Ogac Lake" (variously, "Ogak Lake," "Ogah River," "Oogah River"), *ogak* being the Eskimo word for codfish. This lake is set among rugged hills (Fig. 1) about halfway along the south side of Frobisher Bay. Its position at 62°52′N and 67°21′W is shown on Fig. 2. "Griffin Bay" is applied to a different inlet on contemporary maps, and it appears certain that Ogac Lake with its codfish is unique along this coast and probably in the whole of southern Baffin Island.

In 1951, M/V *Calanus* of the Fisheries Research Board of Canada carried out much of its work in the Frobisher Bay area, under the direction of M. J. Dunbar. On August 4, a party from the *Calanus* took a dinghy over the threshold into the lake and spent a few hours studying what turned out to be a most unusual hydrographic and biological situation. An account of that short survey has been published (Fisheries Research Board of Canada, 1952, p. 109–110) and Dunbar (1958) discussed the limited hydrographic data taken then. The lake was found to consist of three basins separated by quite shallow sills. It was fresh at the surface, but saline (up to 27‰) at depth. It was much

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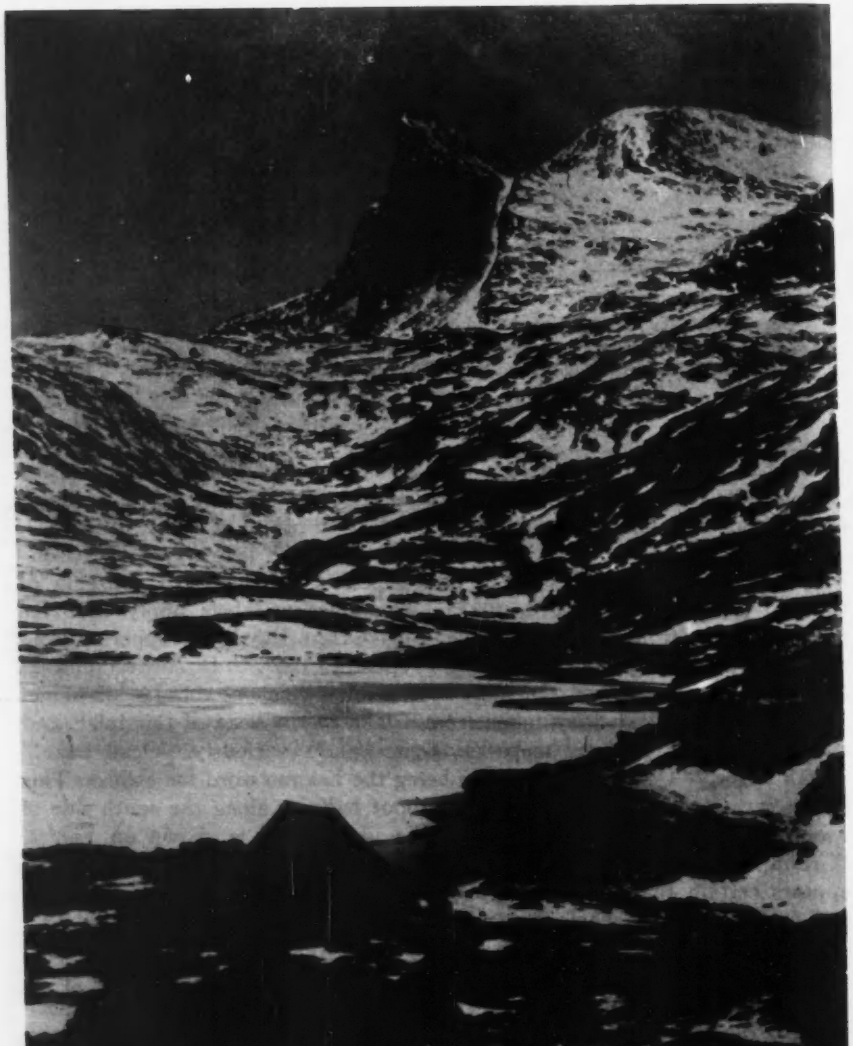

FIG. 1. Camp on the outer basin of Ogac Lake, June 9, 1957.

warmer than the nearby sea and devoid of oxygen in its deeper waters. It was obvious from the setting that the highest tides could flow into the lake, replenishing its salinity, although such an inflow was not observed. A number

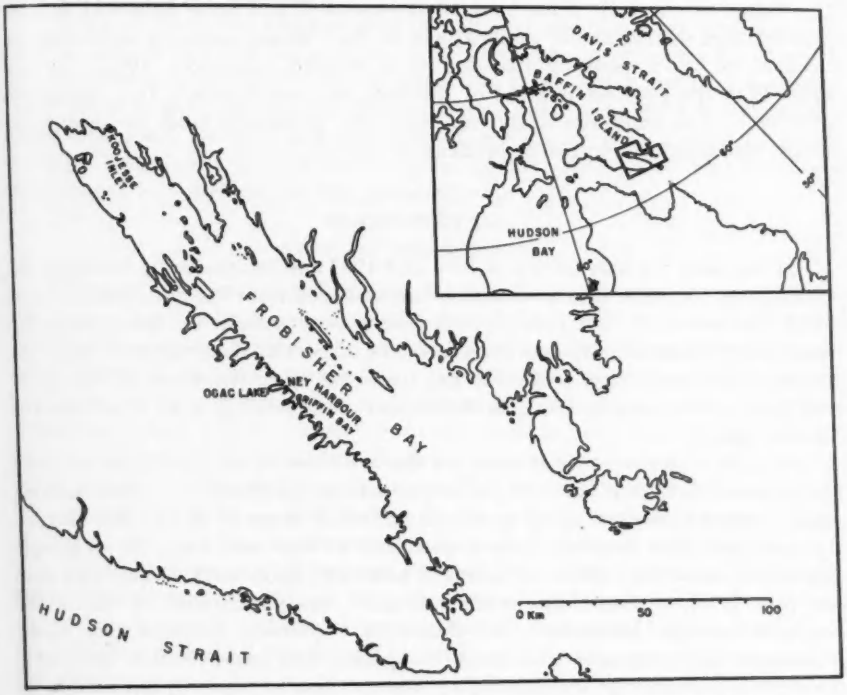

FIG. 2. Map of Frobisher Bay showing place names mentioned in the text.

of codfish were taken and confirmed as *Gadus morhua* L., the Atlantic cod. The fish averaged much larger (one of 128 cm) than their nearest marine counterparts, which migrate north annually to the mouth of Hudson Strait. No cod were taken in Frobisher Bay, and their presense there is hydrographically unlikely. From the circumstances it seemed certain that the fish were relict, presumably from some warmer, postglacial time.

Further study of this remarkable lake and its codfish was obviously called for, and an expedition to the lake in 1952 was arranged by M. J. Dunbar under the auspices of the Arctic Institute of North America and the Carnegie Arctic Program of McGill University. A. D. Dawson and R. S. McCall were taken there aboard M/V *Calanus* on July 16 and picked up August 22. They collected considerable material on the cod, plankton, and benthos of the lake, made regular hydrographic stations, and were fortunate enough to witness the entry of the highest tides of their month's stay. An examination of the planktonic and benthonic material from the 1952 expedition revealed that it consisted of a rather depauperated selection of marine forms that were common in the nearby sea.

Some of the collections have been identified and have appeared in systematic and distributional publications of the *Calanus* series. A semi-popular account of the expedition has also been written (Kennedy, 1953). It was clear that the greatest interest of the lake was not faunistic but ecological, and that more extensive study was desirable, preferably from the beginning of the biological season before breakup of the ice.

1957 EXPEDITION

I had seen the lake briefly in 1951 and 1952 and maintained a considerable enthusiasm for more intensive study, but an expedition was not possible until 1957. On June 1 of that year my wife and I were brought by Eskimos to the lake after a 3-day trip by dog team from the airport at Koojesse Inlet near the head of Frobisher Bay, some 120 km from the lake. We were picked up at the lake by ship and returned to the airport on October 4, after 4 full months at the lake.

Clearly there were limitations on the activities of an expedition as small and isolated as that of 1957. All the equipment necessary for living and working in the period before the shipping season had to be taken in on two dog sledges. Immediately after breakup, only a small rubber boat was available to sample from, but important needs, including a powered canoe, were brought by ship on July 23. The season up to early August was punctuated by occasional visits by military helicopters, but thereafter no outside contacts were made. Breakages and shortages were often hampering and improvisation necessary. In general the program was carried out more or less as planned, but inevitably problems suggested themselves that were beyond the scope of available materials and equipment. The hydrographic and plankton cycles were followed by regular sampling, about biweekly, in the three basins of the lake and in the sea outside. Benthos was collected qualitatively and quantitatively, and much time was spent on the codfish.

The hydrographic and planktonic results of the 1957 expedition were largely analyzed (McLaren, MS, 1961a, b), but have not been formally published at length.

1962 EXPEDITION

Analysis of the 1957 material showed that further observations would be helpful in understanding certain hydrographic and biological properties of the lake. It was especially clear that a study of nutrients was necessary for a more complete analysis of population dynamics and production of the plankton.

Work at the lake in 1962 was again begun on June 1. Two trips from the airport by ski-equipped aircraft allowed much more equipment to be brought than in 1957. My assistant Mr T. R. Welch and I stayed at the lake until August 28, when we left for the airport by Eskimo boat.

Work in 1962 was concentrated on nutrient and plankton cycles in the middle basin of the lake. Large-scale fertilization experiments were also carried out in polyethylene columns. Some study was made of the codfish, especially in an effort to get population estimates. Only a small amount of hydrographic work was done. Benthos was collected quantitatively with the aid of scuba diving during late July and early August by Mr. Welch and Mr. P. W. G. McMullon, who arrived for this purpose on July 16.

SCOPE OF THE STUDIES

The series of studies which will follow this paper are monographic in character. Ogac Lake is a curious and even bizzare environment, and to describe and analyze in detail the events occurring there seems worthwhile in itself. The lake also has interest as a kind of natural laboratory where marine problems can be studied in a lacustrine setting, relatively free from advective influences. The study of aquatic life in the arctic is further simplified because of the slow and synchronous development of populations and because of the small number of species generally involved. For these reasons, the life cycles and growth, production, and population dynamics of certain marine species in Ogac Lake may be described with unprecedented detail and accuracy.

Apart from any special interest they may have, the value of such extreme and unusual environments is that they may clarify relationships that are obscure in a narrower range of environmental conditions. Already data from Ogac Lake have aided mathematical analysis of certain general relationships between temperature, size, development rate, and fecundity of marine zooplankters (McLaren, 1965, 1966a, b). The following series of monographs is thus partly intended to supply useful data for more general studies.

I hope that other workers will be persuaded of the value of carrying out their own studies at Ogac Lake and similar landlocked marine waters.

ACKNOWLEDGMENTS

There will be occasion to thank others in following papers, but mention must be made here of the many people and organizations who aided in the work as a whole. The Fisheries Research Board of Canada supported the expeditions, much of the laboratory work, and my educational leave at Yale University. Among colleagues at the Arctic Biological Station of the Fisheries Research Board I am especially grateful to the former director, Dr H. D. Fisher, who cared for so many of the expeditions' needs when we were in the field, to Dr E. H. Grainger, whose wide knowledge of arctic marine faunas was often helpful to me, and to Dr A. S. Bursa, who gave valuable advice on phytoplankton.

I have drawn freely on field notes and collections made by A. D. Dawson and R. S. McCall during the 1952 expedition.

The enthusiasm and continuing interest of Professor M. J. Dunbar of McGill University, who "discovered" Ogac Lake when I was with him on my

first trip north, were in large measure responsible for my return to the lake in 1957.

Residents of Frobisher Bay, especially our dog-team drivers Simonee and Kalowak in 1957 and our boat captain Mosesee, 1962, extended every courtesy. Helicopter pilots of the U.S.A.F. provided a welcome link with the "outside" in 1957, as did pilots of the R.C.M.P. and Wheeler Airlines in 1962.

Captain Pullen, his officers and men of H.M.C.S. *Labrador* performed the vital functions of resupplying us in July and evacuating us in October 1957. They did so with great efficiency and good humor, and seemed unruffled after launching "Operation Ney Harbour" to discover that "I. A. McLaren and Party" were me and my wife in a tent.

At Yale University, my Director of Studies, Professor G. E. Hutchinson, and Professors E. S. Deevey and G. A. Riley gave much knowledge and understanding. On the trip back to the lake in 1962 I attempted to make use of some of the things I had learned from them.

T. R. (Danny) Welch was an admirable assistant in 1962 who neither balked at 16-hr days nor was depressed when the weather prevented any work, and who always ended our days with songs and his guitar. P. W. G. (Bill) McMullon and Danny Welch cheerfully scuba-dived in water which I found very untempting.

A Fellowship from the Canada Council gave me the time and freedom to finish and begin writing up these studies.

Finally, I am most of all indebted to my wife, Bernice, who was my sole companion and assistant at Ogac Lake in 1957, and who helped me make that season uniquely cherished among several in the north.

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Physical and Chemical Characteristics of Ogac Lake, a Landlocked Fiord on Baffin Island[1,2]

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ABSTRACT

Ogac Lake is the small (148 ha) landlocked head of a fiord with three distinct basins. It receives highest spring tides (maximal range 12 m, as high as 1.2 m above lake level) monthly during the open-water season through a narrow entrance. The predictable inflows displaced about one-quarter of the lake's volume in 1957. The lake is meromictic, fresh at the surface and 28‰ salinity at depth. Some 55 kg/m² salt lost in surface outflow in summer was more than restored by the tides by the end of 1957. Deep salinities did not change between 1951 and 1962. Vertical attenuation of light is adequately accounted for by chlorophyll alone. The lake is much warmer than the nearby sea. Temperature inversions are caused by cold tidal water and perpetuated by vertical stability. The gross annual heat budget in 1957 was 22,000 cal/cm², about the same as in the nearby sea, but higher than in a freshwater lake. Heating from below a few meters to 30 m can be accounted for by radiation alone. About 20% of radiation reaching the bottom subsequently appeared as heat in the water immediately overlying the bottom, thus implying restricted horizontal transfer. Oxygen was absent below 25–32.5 m, which may approximate the compensation level in this and similar lakes. Oxygen differences between basins are partly controlled by morphometry. Distinct oxygen minima in 1957 were associated with temperature minima and caused by concentrations of zooplankton. Vertical distribution of *p*H parallels that of oxygen. Specific alkalinities seem slightly higher than in normal seawater. Phosphate showed a distinct and stable minimum just above the anoxic layer and was as high as 14.3 μg-at/liter within that layer. Nitrate was relatively low and maximal just above the anoxic layer. Although nutrient levels seemed partly related to morphometry in the three basins, no evidence of nutrient enrichment of bottom water was found in late summer. The tides contribute negligible nutrients to the lake. The character of Ogac Lake compared with similar lakes derives from the great tidal amplitude and narrow connection with the sea, as well as from its small size and sheltered setting.

INTRODUCTION

Ogac Lake is a member of a class of waters that Strøm (1936) has studied extensively in Norway. Occurring as they do in lands rebounding from glaciation, a whole sequence of types can be found, from somewhat badly ventilated fiords to lakes well above sea level with trapped seawater in their depths (Strøm, 1961).

The south coast of Frobisher Bay, which still has two small ice caps some 60 km to the southeast of Ogac Lake, is almost certainly rising, perhaps rapidly. Mercer (1956) found strand lines along this coast commonly at about

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[2]The second paper in a series of studies of Ogac Lake.
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20 m above high tide, but was convinced of the presence of much higher ones, up to 435 m. Other parts of the Canadian Arctic Archipelago may be rising at 1–2 m per century (Sim, 1960). Ogac Lake is only slightly below the level of the highest spring tides. Many other such semi-isolated waters receive their seawater irregularly or even catastrophically, but the large amplitude of tides in Frobisher Bay is responsible for a regular, measurable, and predictable inflow.

Since Ogac Lake lies in the drainage basin of a small river, there is much freshwater influence at its surface. Ogac Lake is in fact meromictic, with all the attendant peculiarities, and is an example of coastal ectogenic meromixis in the terms of Hutchinson (1957).

Vertical stability is common to all such semi-landlocked fiords, but few are permanently meromictic almost from the surface, like Ogac Lake. The small size and sheltered setting of the lake and its division into distinct basins all serve further to inhibit vertical (and horizontal) movement. This dynamic simplicity makes Ogac Lake an ideal natural laboratory for the study of a number of physical and chemical processes common to all aquatic environments. The present paper has made only small use of the possibilities of Ogac Lake, but may be taken as useful background for more particular physical and chemical studies and for many of the biological problems to be discussed in later papers of this series.

GENERAL METHODS

An outline of expeditions to the lake by A. D. Dawson and S. D. McCall in 1952, and by the author and assistants in 1957 and 1962, was given in the introductory paper of this series (McLaren, 1967). Methods used at the lake were to some extent limited by the remoteness of the site and the difficulties of transport. A 110-v generator permitted more varied work in 1962.

Salinities were measured by hydrometers, checked by occasional samples titrated later. The titrated samples suggest a maximum (2 σ) error of $\pm 0.8‰$ in hydrometer determinations.

Temperatures were determined with a 200-ft bathythermograph (BT) in 1957. Two or more temperatures were taken at critical depths with a reversing thermometer on a "fisherman's frame" with each BT drop. This allowed correction for the mild hysteresis which the BT exhibited. Unfortunately the bathythermograph taken in 1962 was not working from the beginning, and temperatures (often at 1-m depth intervals) had to be taken with reversing thermometer alone.

Light measurements were made in 1962 with a submarine photometer equipped with a Weston photovoltaic cell. The cell was equipped with a standard luminosity filter, restricting its sensitivity to about 450–700 mμ, with a peak at 550 mμ, and calibrated for foot-candles. The "deck cell" was inoperative, but was unnecessary on the cloudless days on which the instrument was used. Nor was conversion to total radiant energy necessary, as the results are used here in a relative way.

Oxygen was measured by the modified Winkler technique as outlined by Strickland and Parsons (1960). Measurements of *p*H and total alkalinity and calculations of total CO_2 were also made according to methods in Strickland and Parsons, using a Beckman model G meter.

Phosphate, nitrate, and nitrite were all determined by techniques given in Strickland and Parsons (1960), except that a Klett–Summerson electrical colorimeter with appropriate filters and solution cells was used instead of a spectrophotometer. Two or three standards were run with all sample batches. The constant and very un-arctic temperatures required for nitrate determination were supplied by a large insulated water bath, which could be replenished with warm water through a small tube. Interfering substances often formed during phosphate determination of anoxic waters, after addition of molybdate. These cleared up a few minutes after addition of $SnCl_2$, and could be avoided altogether by aeration of the samples after they were filtered.

Chlorophyll was sampled and extracted according to the methods given by Strickland and Parsons (1960), but measured with the Klett–Summerson colorimeter rather than a spectrophotometer. The instrument was used with the 12.5-mm tubes and red #66 filter, and one Klett unit was taken as 0.28 mg chlorophyll. The vertical distribution of zooplankton was determined by horizontal hauls of a Clarke–Bumpus sampler. Zooplankton carbon was measured using the wet-ashing technique outlined by Strickland and Parsons (1960). These techniques will be considered in more detail in a later paper on zooplankton.

MORPHOMETRY

It will become clear in the appropriate sections that the morphometry of Ogac Lake has important effects on its hydrography and biology. A reasonably thorough plane-table survey was made in August 1957, from which the bathymetric charts (Fig. 1, 2) were drawn up. The shoreline detail was drawn from an enlarged, vertical air photo.

The lake has three distinct basins, which afforded interesting hydrological and biological comparisons. The outer and middle basins are separated by a sill with a minimum free passage of about 7 m, whereas the threshold depth between the middle and inner basins is less reliably estimated as about 12 m (Fig. 2). The lake is surrounded by an almost level shelf which drops off abruptly at about 2 m depth and which appears to result from ice activity around the shores.

The whole lake has an area of about 1,481,000 m^2 (148 ha, 366 acres) and a volume of some 34,360,000 m^3 (Table I). The development of volume of the inner basin is greater than in the other two. The volume to bottom-area relationship is further clarified in Fig. 3, as it has important hydrological and biological consequences.

LAKE LEVEL

Water-level measurements were taken only very irregularly in 1957, and depths were reckoned from the existing surface at all times. Since physical and

FIG. 1. Bathymetric chart of Ogac Lake. Depths in meters.

chemical properties of the lake vary markedly with depth, seasonal changes at a given depth could be distorted by surface-level changes. For this reason, accurate water-level measurements were kept in 1962, and all seasonal changes

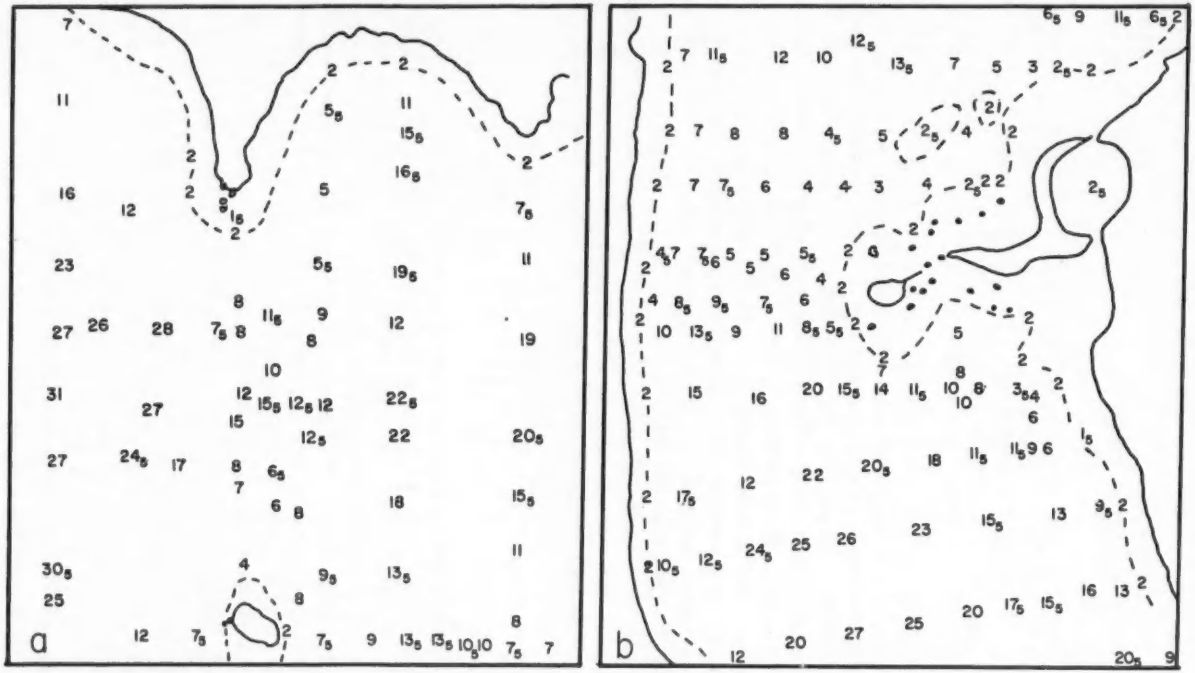

FIG. 2. Available soundings from the vicinity of sills in Ogac Lake separating the inner and middle basins (a), and the outer and middle basins (b). Depths in meters. The limits of the iceworked shelf at about 2 m are shown by broken lines.

TABLE I. Important morphometric parameters of the three basins of Ogac Lake.

Basin	Surface area (m^2)	Volume (m^3)	Mean depth (m)	Max depth (m)	Development of volume
Outer	186,900	2,020,000	10.8	28.0	1.15
Middle	698,200	15,700,000	22.5	60.5	1.12
Inner	596,100	16,630,000	27.9	50.0	1.67

in the water column that year are calculated from the surface datum of the lake in early August, when the lake reached its low summer level.

During the height of the spring runoff in late June 1957, the lake was about 50 cm above the summer level, but fell rapidly thereafter. The winter's snow was much deeper and the thaw much more violent in 1962 than in 1957. Between 1800 hr July 4 and 2000 hr July 5, the lake rose from 11 cm below to 47 cm above the summer datum; it reached a peak of 67 cm above summer datum on the evening of July 6. By the end of July, summer levels were reached, but the rapid thaw resulted in a thicker freshwater layer on the lake through the summer in 1962 than in 1957.

The lake level varied slightly as a result of rains during summer, but incoming tidal water caused considerable changes in lake level. This allowed estimates to be made of amounts of tidal inflow, as will be shown in the next section.

TIDAL INFLOW

TIDAL CYCLE

The tides of Frobisher Bay are among the world's highest with a maximum range of about 40 ft (12 m). No equipment was available for measuring tides of such amplitude, but the cycle was closely approximated from the Atlantic Coast Tide and Current Tables (published annually by Canadian Hydrographic Service, Ottawa, Canada). High tides in three localities in Frobisher Bay are given as height corrections on the predictions for Diana Bay, Hudson Strait, in the tide table for 1962. When reduced to the mean sea level given for each locality, the corrections are almost the same: +2.5, +2.5, and +2.4 ft for mean tides, and +3.1, +2.9, and +1.6 ft for large tides. Mean sea level at Diana Bay is given as 17.7 ft above datum, so it is assumed that height of large tides above mean sea level at Ney Harbour may be calculated by subtracting 15.2 ft (17.7–2.5) from values for Diana Bay in the tide tables.

Another correction is needed before the tide tables for Diana Bay can be used. The "lag" of the tide differs by about 10 hr in the two localities, and the highest spring tide should fall about 10 hr earlier in Ney Harbour (N. G. Gray, Dominion Hydrographer, *in litt.*). Thus high-tide levels from the tables must be plotted against time, joined by a smooth curve, and shifted +10 hr on this curve.

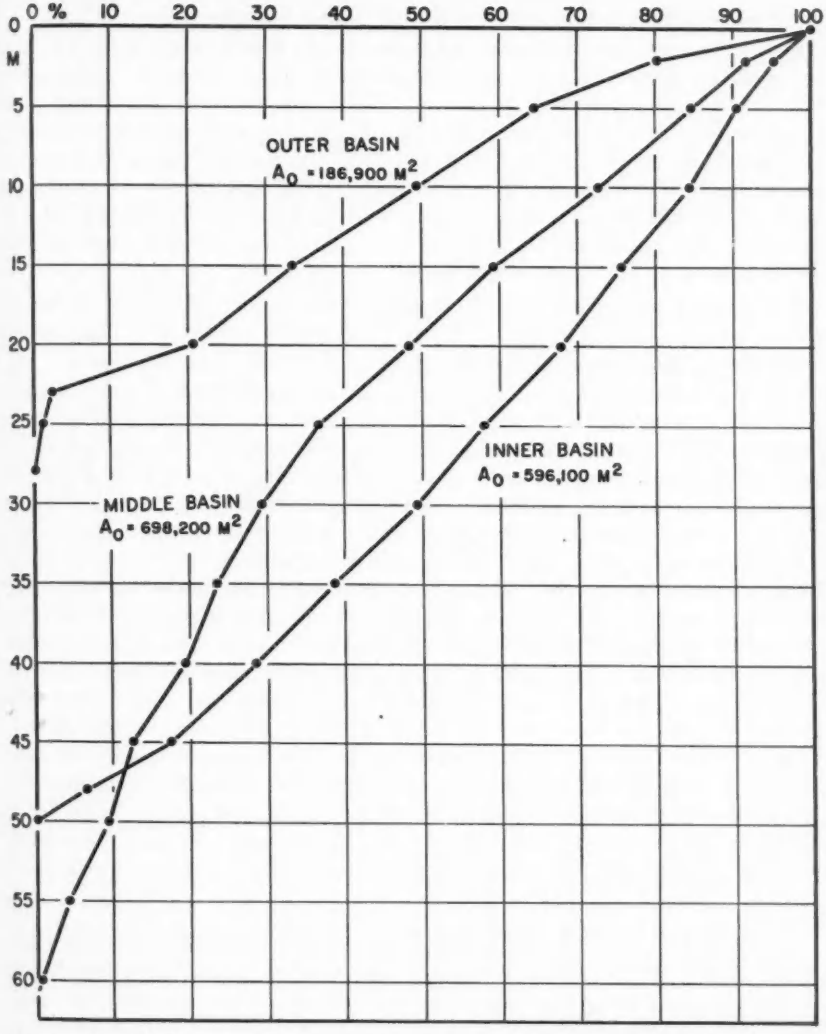

FIG. 3. Relationship between depth and areas within depth contours (as a percentage of surface area, A_o) in the three basins of Ogac Lake.

The calculations show only slight inequality between the semidiurnal tides at Ney Harbour, but the new-moon spring tides may exceed the full-moon tides by over 1.5 m, and the equinoctial tides may be higher than those of the solstices by more than 1 m.

Amount of Inflow

The highest tides at Ney Harbour exceed the level of Ogac Lake by little more than a meter, and the lake thus receives only the new-moon spring tides. The small spring tides of the winter solstice are probably prevented from entering the lake, which freezes to the bottom near the entrance. However, ice barriers may not always exclude the large tides of the spring equinox. In early June 1957, the ice around the entrance and edges of the lake was anchored fast, but in 1962 the lake ice had many holes and fissures. The spring tides of June 1–5, 1962, only entered the lake very feebly, and the disruption of lake ice was probably due to the much higher tides of April.

Attempts were made in 1957 to measure the incoming current across its widest section. The high velocity (up to 2.1 m sec^{-1}) and the irregular channel made this approach somewhat dangerous and the results of little value.

It was much simpler to measure rises in lake level, which can derive from only two sources — tidal inflow and freshwater drainage into the lake. In August 1952, several days after a series of tidal inflows, rough estimates of current velocity and depth were made at 5-m intervals across a 42-m section of the freshwater effluent (fieldnotes, A. D. Dawson and R. S. McCall). These revealed a freshwater discharge rate of about 1100 m^3 hr^{-1}, which would contribute only about 0.7 mm hr^{-1} to the rise of the lake during tides. No other measurements of freshwater outflow have been made, but an indication of the maximum probable contribution of fresh water can be gained indirectly. Before the spring-tide series of late September in 1957, the lake level was very low and freshwater outflow had almost ceased. Heavy rain and snow occurred near the end of the tidal series but the lake level rose before this, as tidal increments were incompletely discharged between the semidiurnal inflows. This made it possible to measure fall of the lake as a function of lake level at a time of little freshwater influence. The following representative values were obtained from drops in lake level (datum on September 22) over periods of 1.2–1.7 hr.

Average height above datum (*cm*)	23	32	43
Rate of fall (*mm* hr^{-1})	6	12	22 .

Although the lake was very much higher during the spring melt (see Lake Level, above), it fell rapidly thereafter, and was less than 20 cm above the summer datum level by the late July tides of 1962. The maximum recorded rises in the lake after summer rains were 11 cm in 1957 and 7 cm in 1962. Clearly, the contribution of fresh water to the lake during tides was at most a few millimeters per hour. Since the observed hourly rises of the lake during tides varied between about 5 and 105 mm, the effect of fresh water is safely ignored, and volumes of inflow can be calculated from lake rise and lake area.

The relationship between calculated volumes of inflow and predicted heights of tide is shown on Fig. 4. The curve was fitted by eye to points for calm or nearly calm days, which clearly deviate less from the curve than those for windy days.

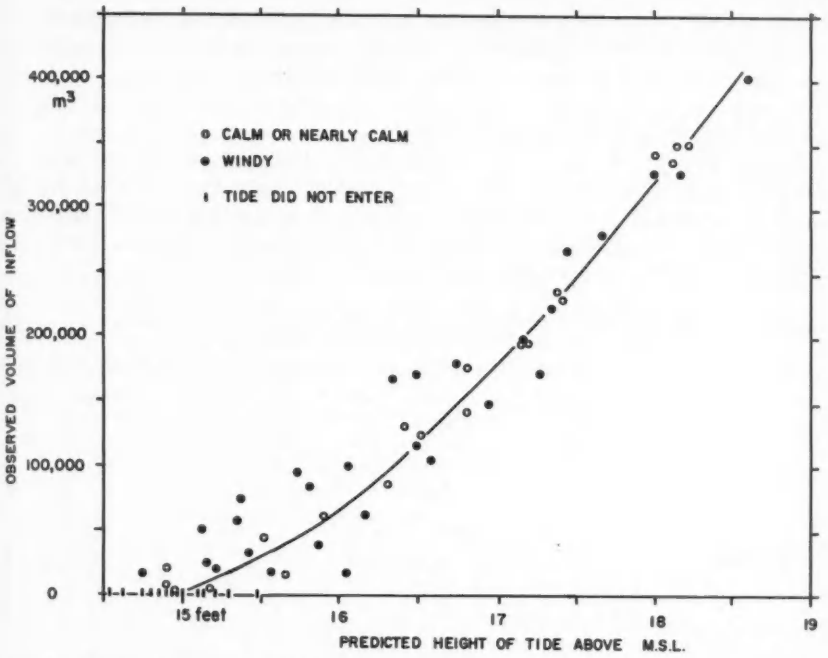

FIG. 4. Relationship between tidal height above mean sea level and amount of water entering Ogac Lake.

The volumes for each tidal series in Table II are largely based on observed rises of the lake. The tide tables and the curve on Fig. 4 were used to calculate volumes of 11 inflows in August and September 1957, which were not actually observed; 7 of these were on calm days and the estimates should be reliable. Late October tidal heights from the tide tables were likewise converted to

TABLE II. The amounts, salinities, and temperatures of tidal water entering Ogac Lake during 1957. Calculated as discussed in text.

Tidal series	Volume of inflow ($m^3 \times 10^6$)	Mean salinity (‰)	Mean temperature (C)
June 28–July 1	0.47	22.0	−0.34
July 26–Aug. 1	1.17	24.5	1.61
Aug. 24–Aug. 30[a]	2.46	ca. 30	ca. 2.5
Sept. 22–Sept. 28	2.57	32.1	−0.11
Oct. 22–Oct. 27[b]	1.80	ca. 33	ca. −1.7

[a]Based on values for Ney Harbour.
[b]Based on assumed winter values.

amounts of inflow, with less assurance of accuracy, since weather conditions were unknown. About 8,400,000 m³, or one-quarter the lake's volume, entered in 1957, most of it during the August and September tides.

Temperature and Salinity of Inflow

The quality of the surface waters of Ney Harbour (Table III) is as important as the quantity of tidal inflow in determining the character of Ogac Lake. Not only is there a decrease of salinity in early summer, but the surface waters are more strongly stratified then. Temperature increased until early September, after recovery of surface salinity.

Table III. Salinities and temperatures of near-surface water in Ney Harbour in 1957. Depths in June are below bottom of ice.

	Depth (*m*)	June 7	June 23	July 6	July 21	Aug. 7	Aug. 20	Sept. 6	Sept. 26
Salinity (‰)	0	31.2	5.8	1.9	7.5	27.2			
	1		33.3						
	2			8.9					
Temperature (*C*)	0	−0.8		0.2	2.2	1.3	2.5	3.2	1.2
	1		−1.1	0.8		0.4	1.8	2.6	0.2
	2					0.2	1.4	2.0	−0.1

Figure 5 shows that the salinity of a large inflow on June 30 greatly exceeded that of a smaller inflow the next day, whereas in late September, when

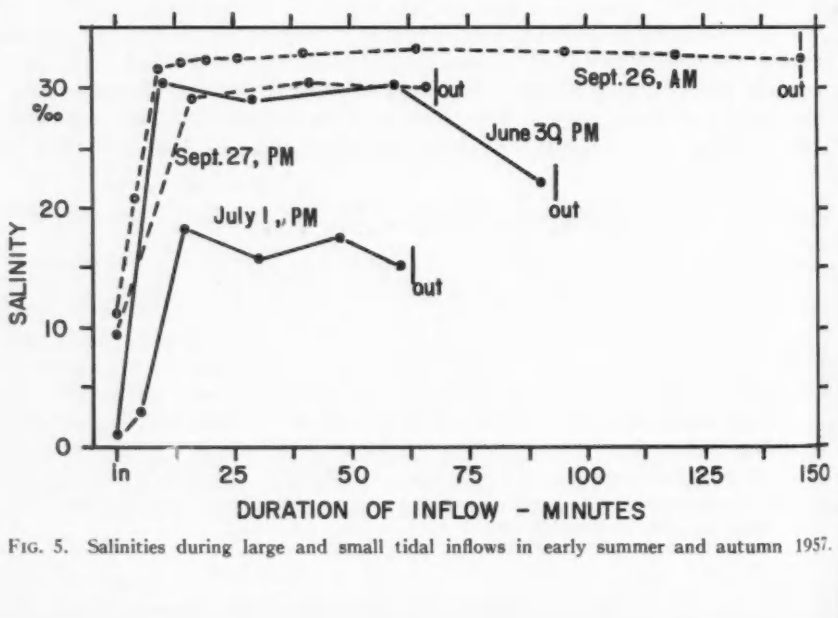

Fig. 5. Salinities during large and small tidal inflows in early summer and autumn 1957.

surface waters are not strongly stratified, the salinity of a large inflow differed little from that of a smaller one. Since little water actually enters the lake near the beginning or end of an inflow, it seems safe to use average threshold values where available (as from Fig. 5) or even single values from mid-tide as measures of the salinity or temperature of the whole inflow. Such values were used to construct Fig. 6, which was in turn used to calculate average temperatures and salinities of inflows during three spring-tide series in 1957 (Table II). Unfortunately, pertinent observations were not made of the late August inflows, but the upper meter of water in Ney Harbour (Table III) from which the inflows were derived averaged about 2.5 C and probably had a salinity of about 30‰, slightly less than that of the late September inflows. Tidal inflows in late October are assumed to have had salinities and temperatures close to the winter values of 33‰ and −1.7 C.

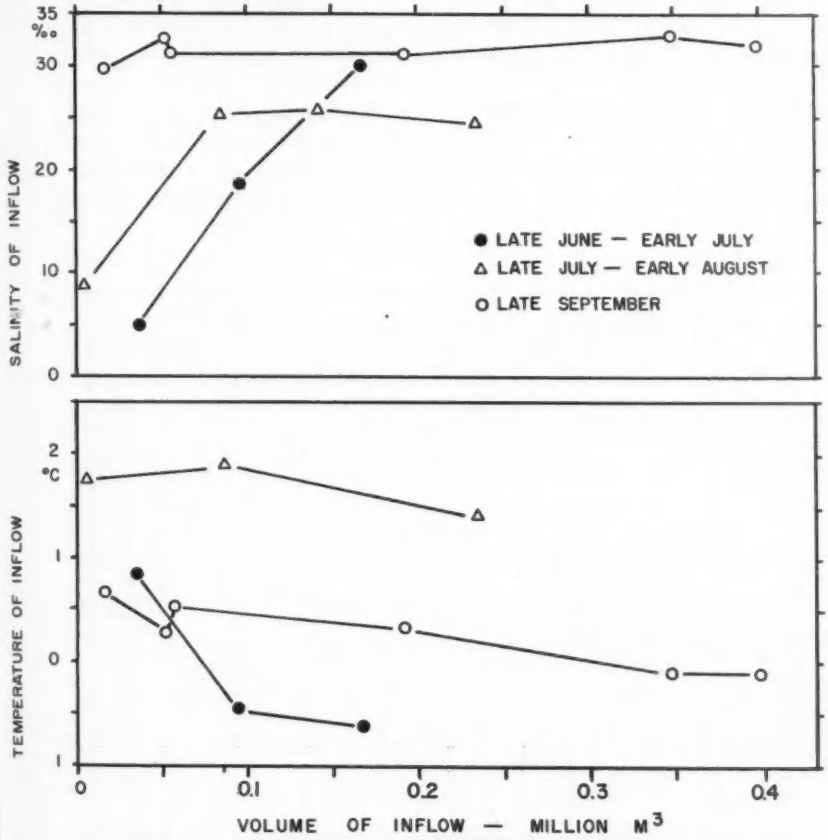

FIG. 6. Relationship between volume of inflow and its mean temperature and salinity during tidal series at different seasons in 1957. See text.

The density of the inflow determines its fate in the lake. After gaining some fresh water by mixing at entering, tidal water flows into an equivalent density stratum in the outer basin. If this stratum is shallower than about 7 m, tidal water can pass over the sill and seek its equivalent density level in the middle basin; if this layer lies above 12 m, tidal water can enter the inner basin (see Fig. 2). Alternatively, tidal water may penetrate deeply in the outer basin and therefore displace lake water over the sill into the middle basin. Since the density is overwhelmingly determined by salinity, the extent and depth of penetration of tidal and displaced water can most easily be followed from temperature changes, as will be shown in the section on temperature.

SALINITY

The effect of fresh water running into Ogac Lake is only partly offset by tidal inflow, and the lake is less saline than the sea outside. As might be expected, the outer basin is most saline and the inner basin least. The divergences in salinity (Fig. 7) occur below the levels of shelves separating the basins (cf. Fig. 2).

Downward mixing of fresh water increases stability in summer, and warming has a similar, if smaller, effect. It will be shown from temperature effects that tidal inflows seek their own density levels, and therefore cause little vertical mixing. The lake is clearly permanently meromictic below a

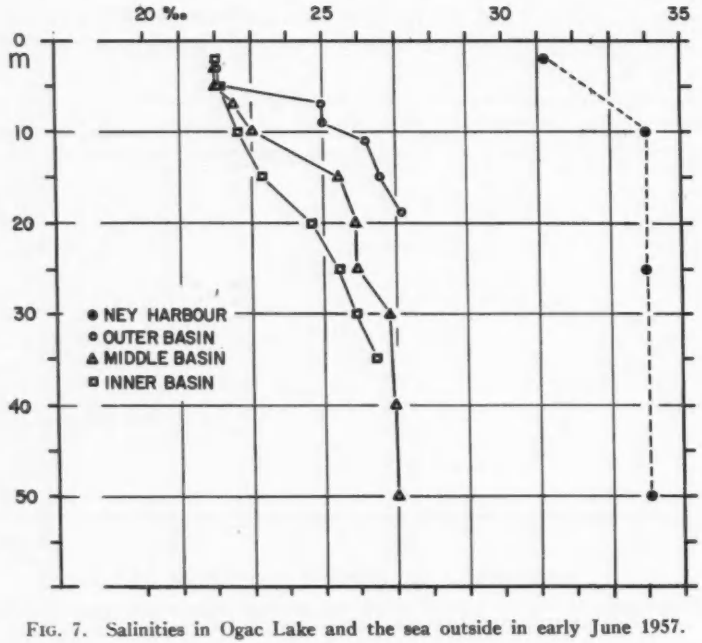

FIG. 7. Salinities in Ogac Lake and the sea outside in early June 1957.

freely mixing, fresh layer which develops in the top few meters in summer.

Seasonal changes in salinity are outlined by selected curves on Fig. 8. The scatter of points in deep water, below freshwater influence and not affected by tidal inflows, must reflect inaccuracies in the hydrometer determinations (see General Methods). Such inaccuracies, together with the wide spacing at critical depths and times, and the lack of datum corrections, do not allow calculation of vertical diffusivity coefficients. However, it is possible to describe the salinity cycle in general terms.

Water at the surface of an ice hole was 9‰ on June 4, before melting had occurred; it is assumed in the following calculations that the ice had been completely freshened by the freezing process. By integrating depth-specific volumes and reductions of salinities at 1-m intervals, it is calculated that the lake lost about 28 kg/m² of salt by outflow between June 3–5 and July 2–4. The deficit reached 55 kg/m² on August 3–4, and was greater in the inner (63 kg/m²) and middle (62 kg/m²) than in the outer (24 kg/m²) basin. The outer basin certainly does not offer as much reach for wind-mixing, especially by the strong winds, which follow the axes of the fiord and the middle and inner basins. There is also a suggestion of greater seasonal reduction of salinity at 10 m in the middle basin (Fig. 8). This may have resulted from morphometric advantages for deeper mixing (depth–volume relationships in Fig. 3). Salinity was not again determined in all three basins until September 22, when the overall deficit was 19 kg/m². On September 29–30, after the tides, the lake contained 2 kg/m² more salt than in early June.

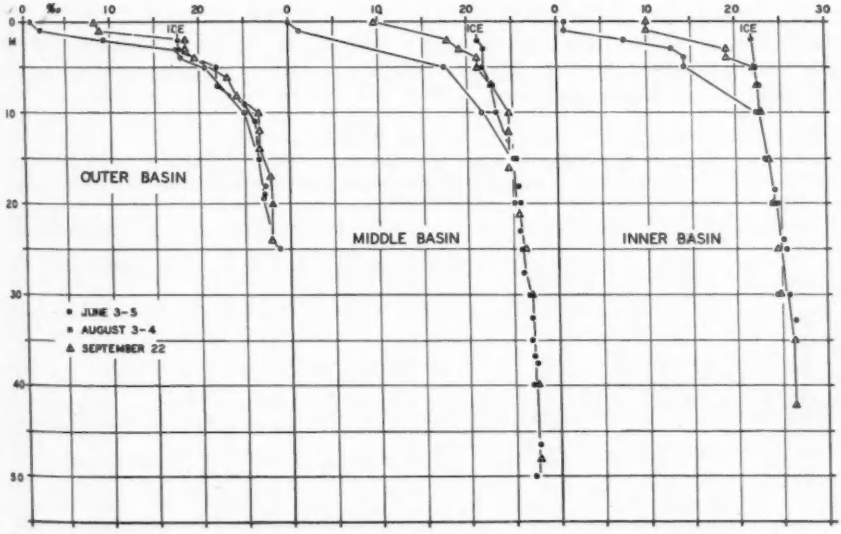

FIG. 8. Seasonal changes in vertical distributions of salinity in Ogac Lake in 1957. Some salinity measurements from below 20 m in mid-June added to those from June 3–5.

Without restorative tides, the lake would continue to freshen. The salt content of tidal series can be estimated from Table II. Each series can be assumed to have displaced an equivalent volume of surface water with a salinity equal to the mean of surface salinities before and after the tides. The estimated salt contribution for July, August, and September was about 97 kg/m².

If the surface salinities of late September were maintained through October, it can be estimated from Table II that a further 26 kg/m² of salt would have been added by the late October tides, leaving the lake with a surplus at the end of the seasonal cycle. Doubtless the annual balance varies from year to year. The maximum deficit of the middle basin was somewhat larger in 1962 (71 kg/m² between June 7 and August 14) than in 1957 (62 kg/m² between June 4 and August 3), and the maximum depth of the freshwater layer was distinctly greater (about 3 m and 2 m respectively). The deeper waters appear to vary little from year to year and no overall trend is shown over a decade (Table IV), although presumably over the long term the land is rising and the lake freshening.

LIGHT PENETRATION

The waters of Ogac Lake are very transparent. Light penetration was measured on two cloudless days in 1962 (Fig. 9). On July 4 there were 35 cm of rather wasted ice. Although more light penetrated the surface in August, it was more rapidly attenuated, so that about the same amount of light reached below 25 m. The photometer (see General Methods) was sensitive only to the visible range, and did not measure the large amounts of incident long-wave radiation. However, much of this radiation is rapidly absorbed by water. Figure 9 probably gives an adequate *relative* picture of the decrease of total radiation below a few meters.

TABLE IV. Salinities (‰) of deeper waters in Ogac Lake, 1951–62. Confidence limits of means are ±95% f.l. Some mean values include estimates based on interpolation from salinities of nearby depths.

Basin	Depth (*m*)	Aug. 4, 1951	July 22–Aug. 18, 1952	June 3–Sept. 29, 1957	June 8–Aug. 22, 1962
Outer	10	27.0	26.5±0.1	25.3±0.2	–
	17–18	27.5	27.7±0.2	27.4±0.1	–
Middle	10	22.3	22.3±0.0	23.1±0.8	23.6±0.1
	25	26.1	26.5±0.2	26.1±0.5	26.3±0.2
	45–50	27.0	27.3±0.1	27.5±0.2	–
Inner	10	–	22.5±0.2	22.5±0.2	–
	25	–	25.8±0.1	24.9±0.4	–
	45	–	26.5±0.2	26.5±0.1	–

TABLE V. Nutrient levels in the middle basin, 1962, in sediments (μg-at/kg) on Aug. 20, and at equivalent depths in the water (μg-at/liter) within ½ m of the bottom on Aug. 17 and in the center of the basin on Aug. 16.

Depth (*m*)	Sediment type	Reactive PO_4–P			Reactive NO_3–N		
		Sediments	Near bottom	Center of basin	Sediments	Near bottom	Center of basin
3.8–4.3	–	–	0.36	0.25	–	Trace	1.1
8.5–9.1	Sand mud	25.1	0.47	0.53	Trace	"	Trace
12.5–13.9	Mud & stones	24.9	0.48	0.65	8.6	"	1.6
17.3–19.1	Mud & stones	9.1	0.91	0.80	3.4	"	0.6
25.6–26.1	Foul mud	27.6	1.44	1.25[a]	Trace	"	0.6[a]

[a]Determined Aug. 21.

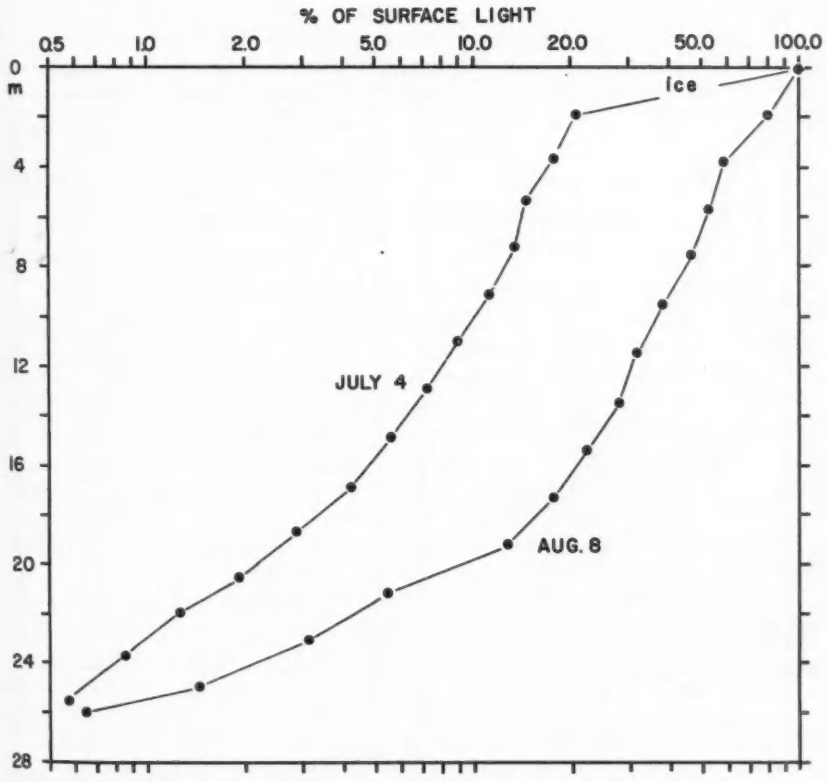

FIG. 9. Attenuation of visible light in the middle basin of Ogac Lake on two dates in 1962.

The attenuation of light appears to be related to the large concentrations of organisms in deeper water. The vertical extinction coefficients (k) in Fig. 10 were determined as usual from

$$I_z = Ie^{-kz}$$

where I is intensity at a given depth, I_z is the intensity z meters deeper, and e is the base of natural logarithms. The values of chlorophyll and zooplankton carbon are unfortunately not for the same dates as the light measurements. The vertical distribution of zooplankton in July was determined from successive vertical net hauls through the ice, and is at best approximate, but values in August are from quantitative horizontal hauls, and are sufficiently accurate to allow an estimate of the relative roles of phytoplankton and zooplankton in attenuating light. The multiple regression equation is as follows:

$$k = 0.027 + 0.086\ C + 0.0018\ Z$$

where k is the extinction coefficient calculated at depths intermediate between those at which light was measured (Fig. 10), C is chlorophyll in mg/m³, and

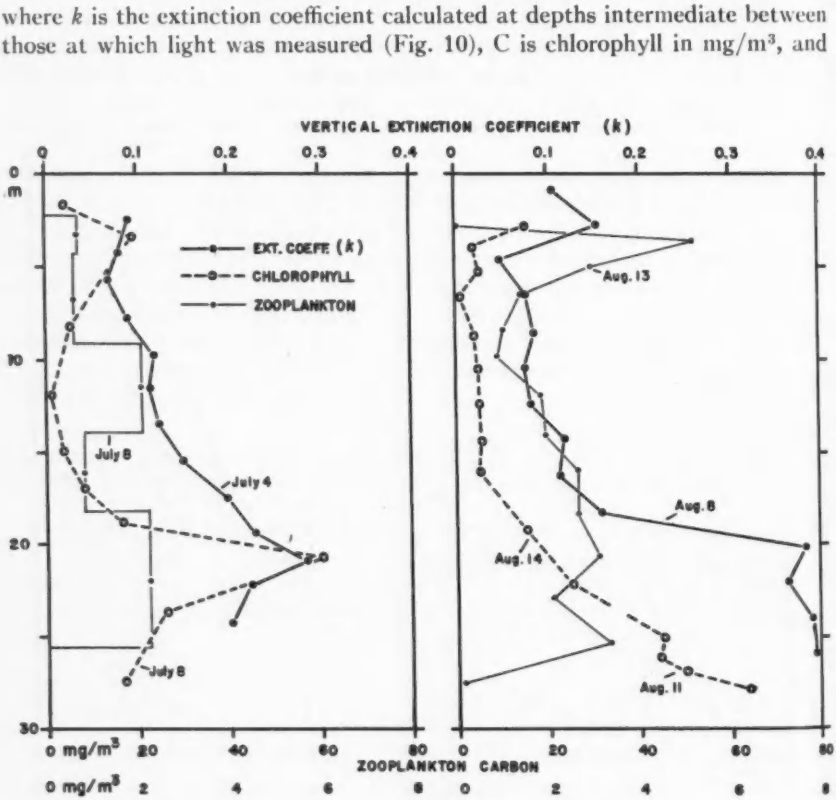

FIG. 10. Relationship between vertical extinction coefficients of visible light on two dates in 1962, and vertical distribution of chlorophyll and zooplankton on nearby dates.

Z is zooplankton carbon in mg/m³. Both C and Z were determined from Fig. 10 for depths at which k was calculated. The coefficient of multiple correlation, $R_{k.CZ}$, is 0.92 ($P < 0.01$). Most of the association comes from the chlorophyll ($r_{kC.Z} = 0.90$).

It thus appears that Ogac Lake differs from most coastal waters in that almost all the attenuation of light is of biological origin. The first term in the equation approximates the true absorption coefficient in water of blue-green light, which probably predominates below a few meters. This is in keeping with the clarity of the freshwater influents in summer and the high stability of the lake, which inhibits inorganic suspension. The effect of chlorophyll on light in nature is well known. The above regression coefficient for chlorophyll is not very different from the more complex expression, $0.0088C + 0.054C^{\frac{2}{3}}$, derived empirically by Riley (1956) from large numbers of observations. A conservative carbon to chlorophyll ratio of 30:1 (Strickland, 1960) implies that zooplankton is about as important as phytoplankton in attenuating light in Ogac Lake. However, the partial correlation coefficient for zooplankton is not significant. This lack of significance may result in part from wide variations in size and optical density, but it also seems unlikely from optical principles that zooplankton could be as important as the equation suggests. The simple regression, using chlorophyll values from July as well as August (Fig. 10), is

$$z = 0.067 + 0.069\ C.$$

and seems quite adequate ($r = 0.79$; $P = 0.01$).

TEMPERATURE

General Characteristics

There are striking differences in thermal properties between Ogac Lake, the sea outside, and a nearby freshwater lake (Fig. 11). The higher temperatures of the lakes are of course due to their small size and landlocked nature, whereas the extraordinary vertical distribution of temperature in Ogac Lake results from cooling by tidal incursions, preserved by the vertical stability of the lake. Each basin is hydrographically distinct, especially below the level of the sill separating it from its neighboring basin (see Fig. 2). The outer basin receives most of the cold tidal inflows, and accordingly maintains colder temperatures. The middle and inner basins may gain cold tidal water, but also receive relatively warm water displaced over the sills between the basins. Therefore they maintain warmer temperatures. Although the mean temperature of the middle basin changed little between 1957 and 1962, the upper waters became warmer and the deeper waters colder. This must be the result of relatively deeper penetration of cold tidal (or displaced) water in the intervening years.

Heat Budgets

When observations were begun in early June of 1957 and 1962, daytime temperatures were just beginning to rise above freezing, and little solar radiation could have penetrated the snow-covered ice. Annual heat budgets may

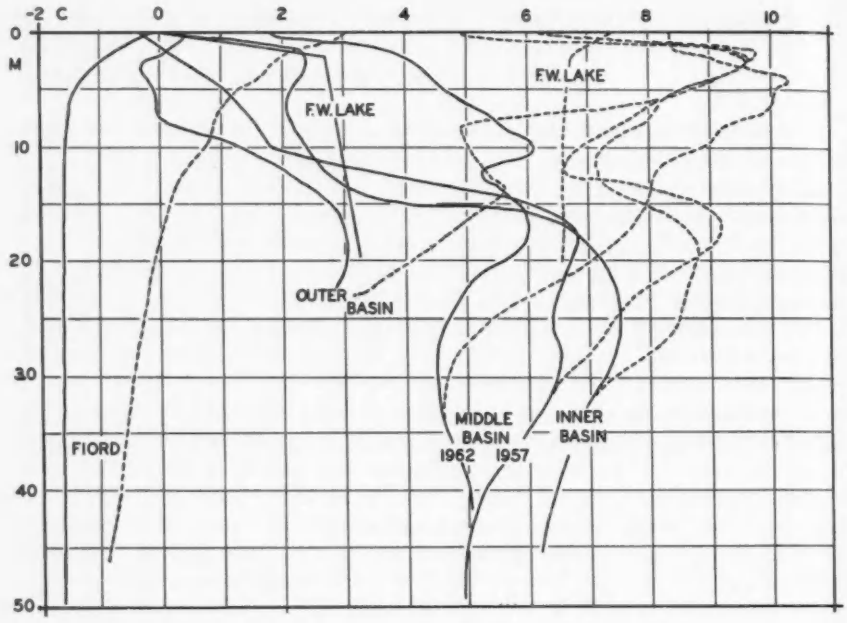

FIG. 11. Vertical distributions of temperature in Ney Harbour (fiord), the three basins of Ogac Lake, and a nearby freshwater lake at the end of winter (——, early June in Ogac Lake and Ney Harbour, July 10 in the freshwater lake) and at the height of summer warming (- - - -, August 11 in the freshwater lake, September 6 in Ney Harbour and September 21 in Ogac Lake in 1957, and August 21 in the middle basin in 1962). All curves for 1957 except as marked.

be calculated from this time of minimum heat content (ignoring warming of the ice-sheet). There are some peculiarities of the lake that require consideration. The lake was considerably cooled after the entry of the tidal water in late August. However, the waters continued to warm after these tides, so that the maximal heat content of the lake (from which the heat budgets are normally calculated) occurred before the tides of late September. No correction is normally made for effects of influents in heat budgets of lakes, but tidal inflows are considered here. Heat budgets are also derived by assuming that temperature at a given depth is uniform, but evidence will be given below for local radiation heating over the bottom of Ogac Lake.

Temperature changes between early June and September 21, 1957, are shown on Fig. 11. Birgean heat budgets (Hutchinson, 1957) were calculated for this period as 8490 cal/cm² for the inner, 8460 cal/cm² for the middle, and 5770 cal/cm² for the outer basin of the lake. To these must be added about 12,000 cal/cm² for the melting of ice, which averaged 148 cm on two basins and on the fiord outside before melting had begun, and which can be considered fresh. The cooling effects of tides were calculated from volumes and temperatures of inflows (Table II) and from mean temperatures of displaced surface

waters before and after each tidal series (see below, Fig. 15). The heat losses were about 10, 660, and 900 cal/cm² for the tides of late June, July, and August respectively. Only 220 cal/cm² were gained by the lake in the week prior to September 21. It is doubtful if the estimated loss of 800 cal/cm² due to the tides of September 22–28 could have been regained later in the season, and the heat content on September 21 may be taken as the seasonal maximum. The gross annual heat budget for the lake, with corrections for tidal cooling, was therefore about 22,000 cal/cm².

The heat budget in 1962 was probably quite similar. The uptake of heat (corrected for tidal cooling, but not for melt of ice) in the middle basin of the lake was about 7100 cal/cm² between June 7 and August 16, 1962, compared with about 8800 cal/cm² between June 4 and August 17, 1957.

These heat budgets can be profitably compared with that of a nearby freshwater lake. This small kettle lake (area 10.9 ha, maximum and mean depths of 24 and 8.9 m, and a development of volume of 1.11) is quite similar to the outer basin of Ogac Lake (see Table II), and morphometry alone is not likely to be responsible for differences in their heat budgets. Most of the heat before the first temperature records on July 10 (Fig. 11) must have gone into melting of ice, which is assumed to have been as thick as on Ogac Lake, but which disappeared on July 17. The temperatures below a few meters on July 10 were therefore probably at their winter minimum. The lake mixed irregularly during summer, for its bottom temperatures were 5.41 C on July 26, 6.61 C on August 11, 5.58 C on September 2, and 6.13 C on September 17, before the low of 4.48 C on October 1. There can be little error in assuming that temperatures on August 11 (Fig. 11) were maximal, and the annual heat budget may be estimated as about 15,600 cal/cm².

The heat budget of Ogac Lake is more similar to that of the sea outside. Temperatures in Ney Harbour increased until September 6 (Fig. 11) and had dropped considerably on September 25, 1957. Linear extrapolation of the temperature curves on Fig. 11 suggests an increase of about 9900 cal/cm² in the water column of Ney Harbour between June 7 and September 6 (depth–volume corrections are of course not possible, but are doubtless negligible in the sea). Together with 12,000 cal/cm² for the melting of ice, this gives an approximate annual heat budget of 22,000 cal/cm², very close to that of Ogac Lake.

The large size of the sea and the unstratified waters of the sea and the freshwater lake allow much more downward mixing of heat. However, it is clear that this is counteracted by their tendencies to lose heat mixed to the surface. Ogac Lake traps a great deal of heat and, if it were not for the cooling effect of the tides, even higher temperatures would be maintained.

Radiation Heating

Perceptible temperature increases occur in summer in Ogac Lake down to below 30 m (Fig. 11). The high stability of the waters must preclude turbulent transfer of heat below a few meters, and the implication is that warming of deep waters is due to radiation.

To demonstrate radiation heating, the amount of incoming radiation must be known. No direct measurements were made, but estimates of clear-day radiation are given by Mateer (1955a) in the form of mid-month isopleths for all of Canada. These estimates are higher than those from other recent sources, but are considered realistic, since some measurements were available to Mateer from Frobisher Bay, 120 km from Ogac Lake. Mateer (1955b) relates incoming radiation in summer to average sunshine. Strictly speaking, Mateer's formula should apply to monthly synoptic records, but probably little bias is introduced by using records kept of days and portions of days which were overcast (36% of clear-day radiation) or sunny (100%) and deriving values for each day accordingly. The daily estimates are unlikely to be accurate but may be combined to give acceptable values for radiation delivered between series of temperature measurements, usually about 2 weeks apart.

Very little fresh water was mixed below a few meters (see previous section under Salinity). If other forms of heating are negligible, and if water overlying a given depth can be taken as optically uniform in time, then the amount of heating below this depth should be proportional to radiation at the surface. Figure 12 confirms this relationship, and implies that about 20% of incident radiation reached below 5 m. Similar analyses show that about 6% penetrated to 15 m and 1.5% to 25 m in the middle basin.

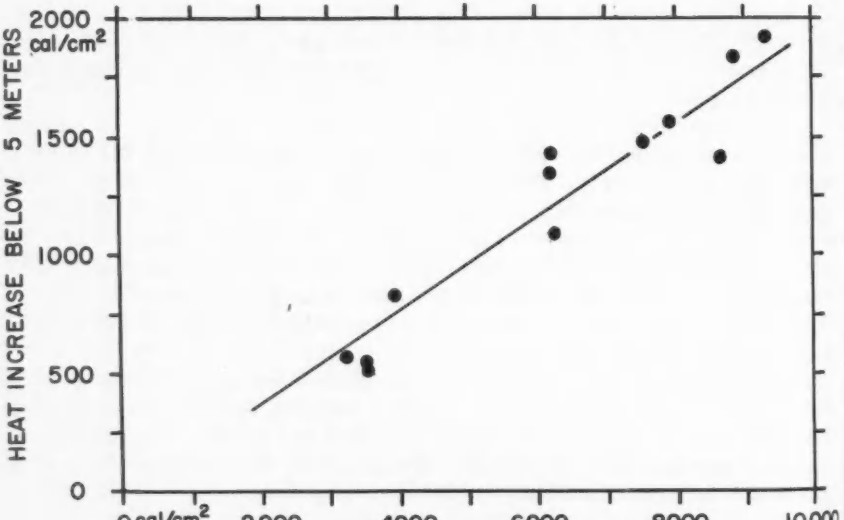

FIG. 12. Relationship between heat delivered at the surface (calculated as described in the text) and heat increases in the water columns below 5 m in the three basins of Ogac Lake. Each point represents a roughly biweekly interval, unaffected by tidal inflows, in the open-water seasons of 1957 and 1962.

Even if heat mixed downward may be ignored, detailed analysis of radiation heating requires measurements that are only partially fulfilled by data collected in 1962. Temperatures were taken by reversing thermometers in the middle basin at depths 1 or 2 m apart on August 7 and 16. Incident energy during this period was estimated from cloud cover (as above) during this period as 3150 cal/cm^2. Estimates of water-surface albedo are tabulated by Roden (1959) for latitude as well as season, and were taken as 7.5% for Ogac Lake. The fresh and very clear surface layer may be assumed to absorb radiation as pure water. From among many similar published estimates, tables and graphs in Hutchinson (1957) were chosen for spectral distribution of daylight and extinction coefficients of pure water. It was thus calculated that 59% of energy penetrating the surface was absorbed in the top 2 m. Below this the photometer may give good *relative* estimates of radiation flux and vertical extinction coefficients on August 8 (Fig. 9, 10), assumed to apply between August 7 and 16. Finally, in common with most authors on the subject, it was assumed that heat reaching the bottom is evenly distributed at that depth.

Figure 13 compares observed heat increments with those calculated at the depths for which extinction coefficients are available (see Fig. 9). The most deviant theoretical point (calculated 1.89, observed 2.53) occurred near the boundary of the fresh layer at 2.7 m, where heat could undoubtedly be mixed down. Although the remaining theoretical points do not agree with the observed curve in detail, the overall agreement is good (test of one-to-one proportionality, $t = 0.55$, df $= 11$, $P = 0.4$). In spite of the many assumptions and approximations, this analysis implies that radiation alone accounts adequately for heating of the water column.

Radiation heating is a familiar phenomenon in meromictic lakes, but has generally been ignored in thermal studies of other lakes. Exponential decreases of temperature and heating rate with depth are taken to imply constant vertical coefficients of eddy conductivity (Hutchinson, 1957). However, Bachman and Goldman (1965) have shown in a sheltered mountain lake that

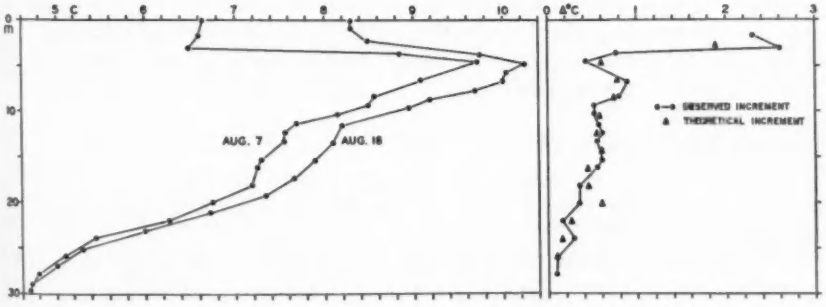

FIG. 13. Relationship between observed heat increases at depths at which temperature was measured on August 7, 1962, and theoretical increases calculated from light extinctions (see text).

heating was almost all due to radiation and also decreased exponentially with depth due to constant vertical extinction coefficients within the narrow range of transmitted wavelengths. Positive departures from an exponential relationship in the hypolimnia of lakes might be explained by increased energy absorption as well as by increased vertical exchange and turbidity currents (see Hutchinson, 1957, p. 476). The non-exponential radiation heating of Ogac Lake (Fig. 13) thus offers a model of what may be more common than generally supposed.

Bottom Warming and Horizontal Heat Transfer

It is evident from a series of bathythermograph records on September 21, 1957, that warming occurred over the bottom where it was sufficiently shallow to receive much radiation (Fig. 14). Presumably the anomalies in the middle basin were eliminated during winter and began to develop at the beginning of the heating season in June. The shallower anomalies in the outer basin must date from late August, when cold tidal water intruded and destroyed the existing temperature structure (see Fig. 15 and discussion below).

The amounts of heat represented by the anomalies at 7.6, 10.4, 21.7, and 22.9 m on Fig. 14 may be estimated by measuring deviations from the temperature curves in deeper water. In order of depth, these amounts are: 200, 120, 170, and 150 cal/cm^2. The amounts of radiation delivered to the bottom can be estimated from warming of the water column below the appropriate depths during the periods under consideration (June 4 to September 21 in the middle basin, August 31 to September 21 in the outer basin). Two assumptions limiting the estimates are: (1) that all heat is evenly distributed horizontally (as was assumed in all previous calculations) or (2) that no heat is transferred from the bottom to the water column. For the above depths, in the same order, these estimates of radiation delivered are: 840–1050, 460–550, 760–850, and 580–650 cal/cm^2. It appears, therefore, that about 20% (range 19–26%) of heat delivered by radiation to the bottom was subsequently lost by buoyant transfer to water just over the bottom. Presumably a smaller amount was absorbed by the sediments. It cannot be assumed that the large portion of heat remaining was in fact evenly distributed by horizontal exchange, and for this reason no attempt was made to modify heat budgets and other calculations involving depth–volume corrections.

Temperature Effects of the Tides

Radiation alone cannot account for the highly anomalous temperature curves in Ogac Lake (Fig. 11), which can only be explained by reference to tidal inflows.

Temperature records are available from immediately before and after each tidal series in 1957, except in late August, when temperature was measured 7 days before the first inflow. Since the density of an inflow is overwhelmingly a function of salinity so that it tends to seek its own salinity level in the lake, the temperature effects are quite startling (Fig. 15).

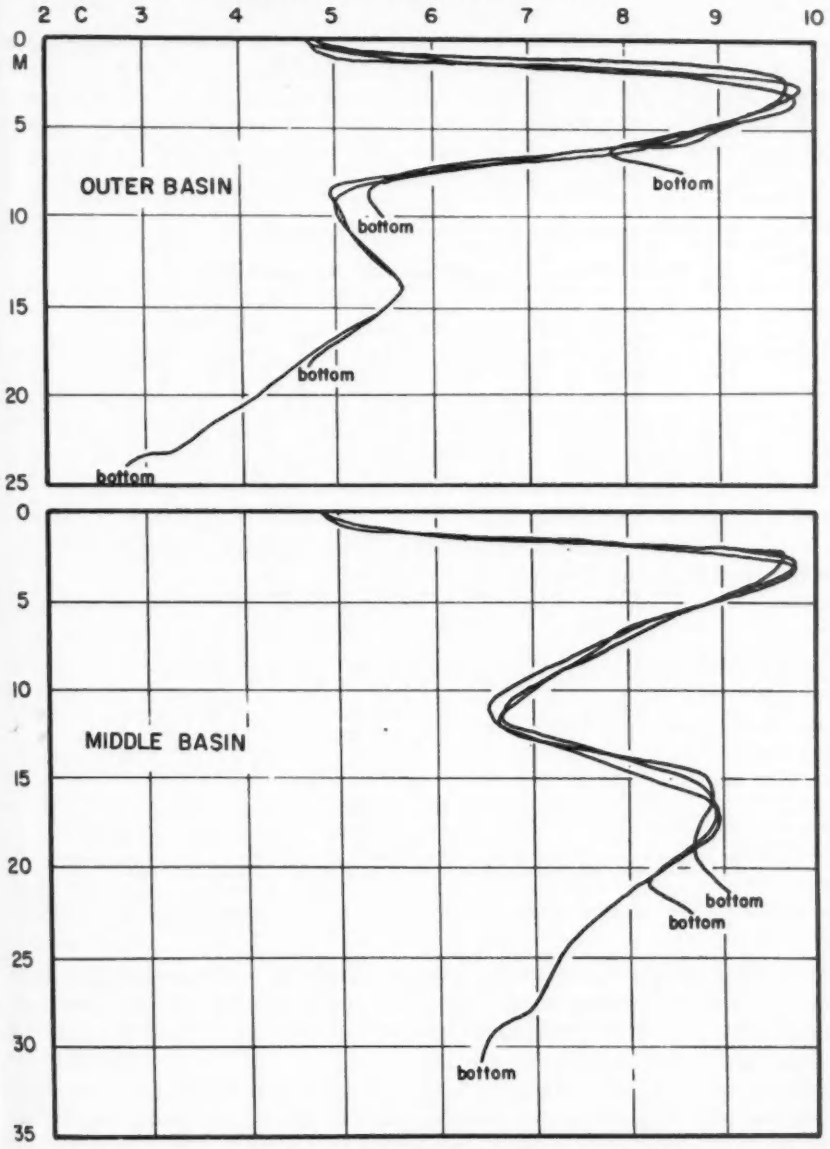

FIG. 14. Evidence of local radiation heating over the bottom of Ogac Lake on September 21, 1957.

The tides in late June had no noticeable effect, even in the outer basin. In late July, the cold-water incursion at 2–3 m was clear in the outer basin, less so in the middle basin, and hardly visible in the inner basin. The incursion

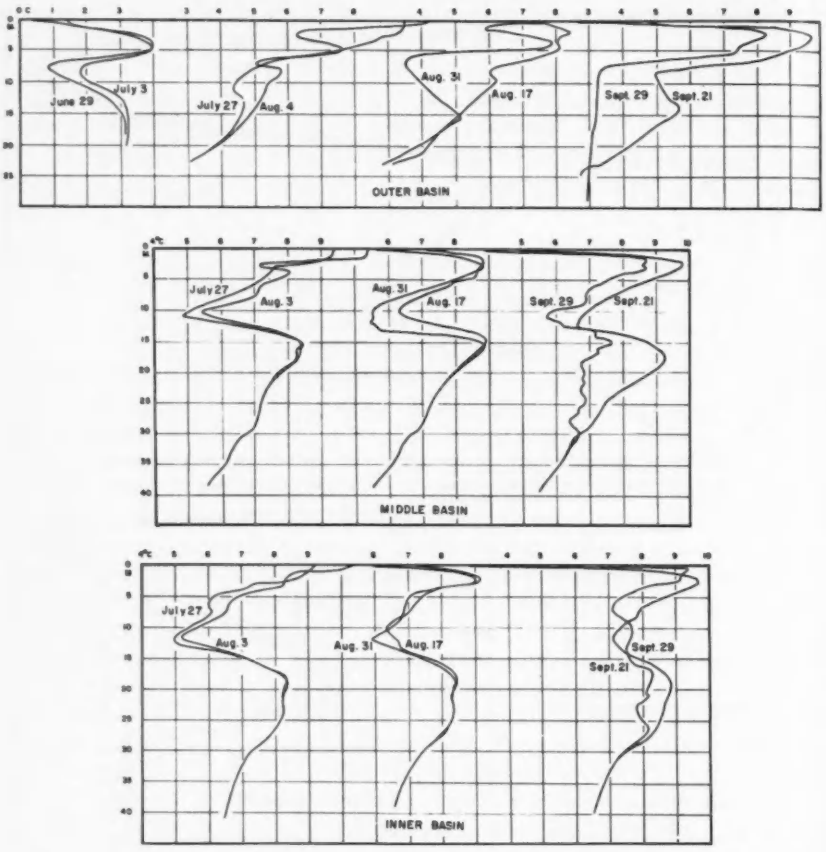

FIG. 15. Vertical distributions of temperature before and after tidal series in 1957.

at 7 m was at about the level of the shelf between the outer and middle basins; therefore its effect in the middle basin was very small. The large inflow in late August caused a strong inversion below 5 m in the outer basin. This allowed some tidal water to flow over the sill at 7 m and expand vertically the pre-existing temperature minimum at 5–15 m in the middle basin. The inner basin was less affected, presumably because much of the water flowing into it was displaced warmer water from the middle basin.

The late September tides had a complex influence quite unlike that of earlier tides. Less dense water reduced temperatures near the surface in all basins, but most of the tidal water, after mixing with some lake water at the entrance, "filled" the outer basin below the 7-m shelf with cold, dense water. Each deep incursion must have displaced successively denser lake water over

the sill into the other two basins, which caused a whole series of temperature anomalies down to about 30 m. The complicated pattern of vertical temperature changes was compounded by horizontal differences (Fig. 16). In general, the further away from the outer basin, the less marked were the anomalies. Presumably what began as coherent flows across the sills mixed and lost momentum as they progressed up the lake at their own density levels.

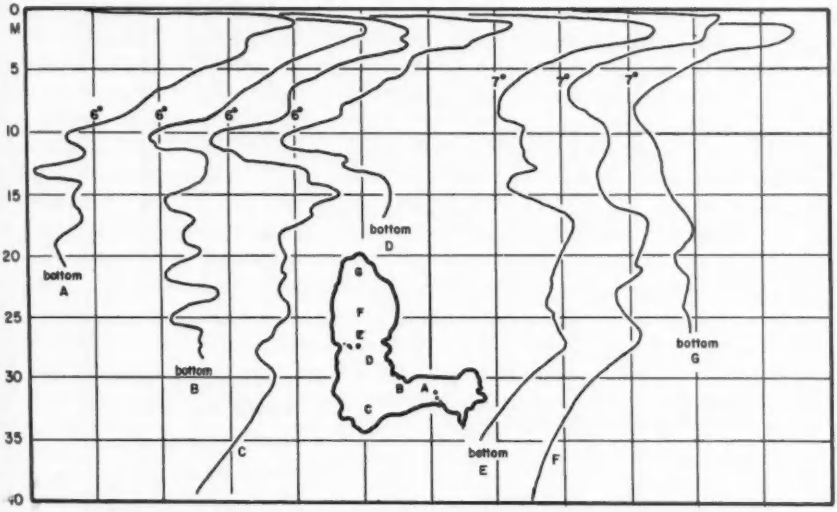

FIG. 16. Vertical distributions of temperature at several stations in the lake on September 29, 1957, after the tidal series. Vertical lines 1 C apart.

The salinity of the last tides of the open-water season must be important in determining the thermal properties of the lake in the following year. If very dense (as implied on Table II) they will displace cool, overlying water from the outer basin to cool the water at greater depths in the other two basins. If late-season precipitation freshens the surface water of the fiord, then cold tidal water will enter the shallows of all basins. These alternative possibilities seem to explain differences at the ends of winter in 1957 and 1962 (Fig. 11) which persisted during the following summers as temperature minima or maxima.

OXYGEN

The vertical stability of Ogac Lake means that seasonal changes in oxygen concentration are almost entirely biological in origin. The discussion in the present paper deals only with vertical distribution of oxygen and differences between basins.

Figure 17 depicts oxygen in the three basins at the end of winter. Oxygen was absent at all times below about 32.5 m in the inner and 31 m in the middle

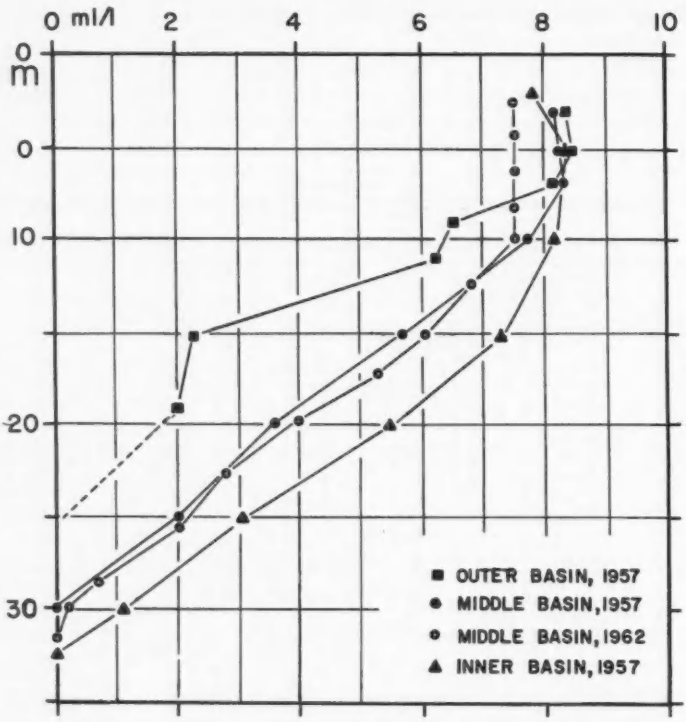

FIG. 17. Vertical distributions of oxygen in the three basins in early June. The broken-line extrapolation is based on later samples from the restricted "deep" of the outer basin.

basin, and was very nearly absent at 25 m in the restricted "deep" of the outer basin. The lake bottom is foul and anaerobic several meters above these depths. The upper limit of the anoxic layer, at least in the steep-sided middle and inner basins, presumably represents a long-term "compensation depth" where phytoplanktonic production matches consumption. It is of some interest to find that the anoxic level of the landlocked head of Winton Bay, about 150 km northeast of Ney Harbour, also begins at about 30 m (30.5 and 31.5 m in two basins). The head of Winton Bay and Ogac Lake are similar in transparency (see section under heading Comparison with Similar Lakes).

Differences in vertical distribution of oxygen between the three basins of Ogac Lake are partly controlled by morphometry, since proportionately more oxidizable seston would reach bottom at shallow and intermediate depths in the outer and middle basins (see Fig. 3). Oxygen changes between June 3–5 and September 14–15, 1957, can be compared for depths greater than 5 m, below which downward mixing is negligible. During this period oxygen increased

in the water columns by 50 cc/cm² in the outer, 41 cc/cm² in the middle, and 10 cc/cm² in the inner basin. It may be that each basin was at roughly the same stage in the seasonal oxygen cycle, but it is not possible to separate oxygen consumption and production, as in calculations of hypolimnetic deficits in lakes (Hutchinson, 1957). Nevertheless, depth–volume corrections reduce the differences between basins to 27, 27, and 12 cc/cm² respectively. The greater development of volume in the inner basin (Table I, Fig. 3) probably has a restricting effect on general productivity.

The middle and inner basins of the lake developed persistent oxygen minima at about 10 and 12 m respectively during the summer of 1957, but no such minima were detected in 1962. Occurrences of metalimnetic minima are well known in freshwater lakes where they have generally been attributed to interrupted fall of seston or to morphometric effects (see Hutchinson, 1957, for a critical discussion). Shapiro (1960) has given ample evidence that an oxygen minimum in Lake Washington results from respiration of large numbers of copepods at the same depth. The oxygen minima in Ogac Lake occurred at the same depths as marked temperature minima (see Fig. 11). The causality is obviously indirect, and it appears that the oxygen minima were caused by concentration of zooplankton at the same depths (Fig. 18). In 1962, when there was no mid-depth temperature minimum, there was no zooplankton concentration, and no oxygen depletion. The zooplankton concentration at 10 m in the middle basin in 1957 consisted largely of copepods, which probably have much higher oxygen consumption, weight for weight, than the zooplankton of the deeper maximum (Fig. 18), which consisted mostly of larger forms such as chaetognaths.

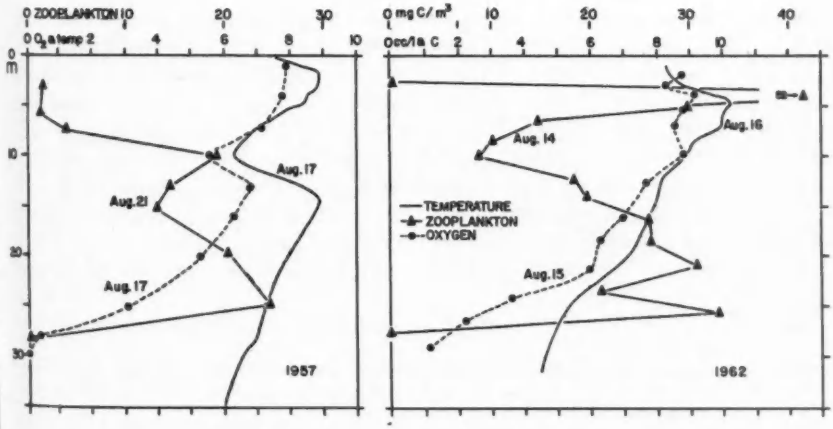

FIG. 18. Relationships between the vertical distributions of temperature, zooplankton, and oxygen in the middle basin of Ogac Lake.

*p*H AND ALKALINITY

Distribution of *p*H in the water column of the middle basin at the end of the 1962 season closely paralleled that of oxygen (Fig. 19). The water was nearly neutral at the fresh surface and at the anoxic boundary. These features have been found in other stagnant fiords (Strøm, 1936).

Total alkalinity measurements from the same data were used to calculate total CO_2 (all forms). As might be expected, total CO_2 paralleled salinity closely (Fig. 19). Specific alkalinity (total alkalinity/chlorosity) averaged slightly higher at all depths (from about 0.126 at 4 m to 0.134 at the anoxic level at 31 m) than the usual seawater value of about 0.123. Part of this might be due to hydrometer errors, but higher specific alkalinities are expected in such waters, and Richards (1965b) has found similar values in Nitinat Lake, British Columbia.

DISSOLVED INORGANIC NUTRIENTS

Extensive seasonal data on nutrients were obtained in 1962, especially from the middle basin of the lake. Only the more general aspects are treated here.

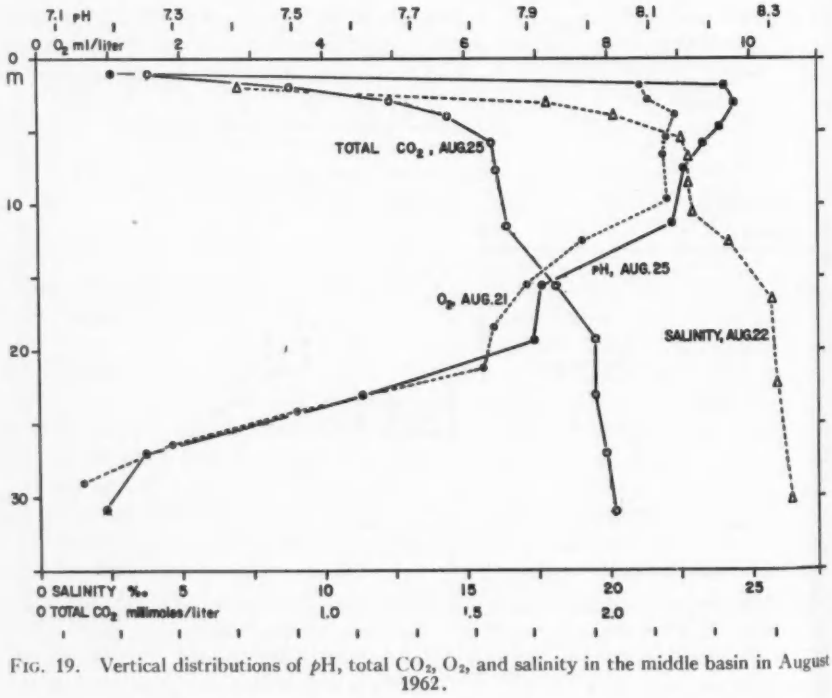

FIG. 19. Vertical distributions of *p*H, total CO_2, O_2, and salinity in the middle basin in August 1962.

Vertical Distribution of Phosphate

A few phosphate measurements were made by A. D. Dawson in late July and early August 1952. These revealed a marked increase of phosphate with depth in the three basins, from 0.4–0.8 μg-at P/liter at 10 m to 1.0–2.1 μg-at P/liter at 17 to 25 m. Values were not obtained from deeper, anoxic water.

Figure 20 shows the vertical distributions of phosphate in the three basins at the end of winter 1962, before the beginning of the productive season. The pattern is similar to that found in other anoxic fiords (Strøm, 1936; Carter, MS, 1963; Richards, 1965a, b). Phosphate increases with depth and reaches very high values in the anoxic water. The highest concentration noted (14.3 μg-at/liter at 18.7 m in the outer basin on June 12) appears to exceed any published figures for unpolluted waters.

A distinct phosphate minimum was noted just above the anoxic layer in the middle basin on June 10. Samples from the other two basins (Fig. 20) were probably not properly spaced to detect such minima, if they occurred. Detailed sampling on three later dates showed that the minimum was a real and stable feature of the middle basin, although somewhat constricted later in the season (Fig. 21). The explanation of this phenomenon remains obscure, although it is worth noting that zooplankton reaches its lower limit at about the same depth, whereas chlorophyll continues to increase into the anoxic layer (see Fig. 10).

Vertical Distribution of Nitrate and Nitrite

Unlike phosphate, these ions are readily reduced by denitrification, and the nitrate maximum occurs above the anoxic depths (Fig. 20). It is in fact surprising to find detectable quantities of nitrate on the only occasion it was analysed in anoxic, sulfide-smelling water (Fig. 21). It is possible that nitrite (the method is based on reduction of nitrate to nitrite) was being measured, as this is known to increase at the boundary of anoxic waters, where nitrate decreases (Richards, 1965a, b). Unfortunately, nitrite was measured only once, and not below 28.4 m, at which depth only traces were found. Neither ion should exist at equilibrium conditions in anoxic water, and further study of the boundary of anoxic waters would be worthwhile.

The highest values of NO_3–N in the lake were considerably smaller than those recorded in seawater elsewhere. The P/N ratio in seawater is usually of the order of 1:10. The much higher ratios implied on Fig. 20, even in shallower water, are typical of stagnant fiords (Richards, 1965a, b).

Nutrients in Sediments and Bottom Water

Bottom grabs were made in mid-August 1962, for nutrient analysis. To do this, 25 g of wet, superficial sediments were mixed thoroughly with 250 cc of artificial seawater, and allowed to settle. The water was decanted, filtered, and analysed for reactive phosphate and nitrate (Table V) in the usual way. In spite of the large amounts of phosphate in the sediments, there was no

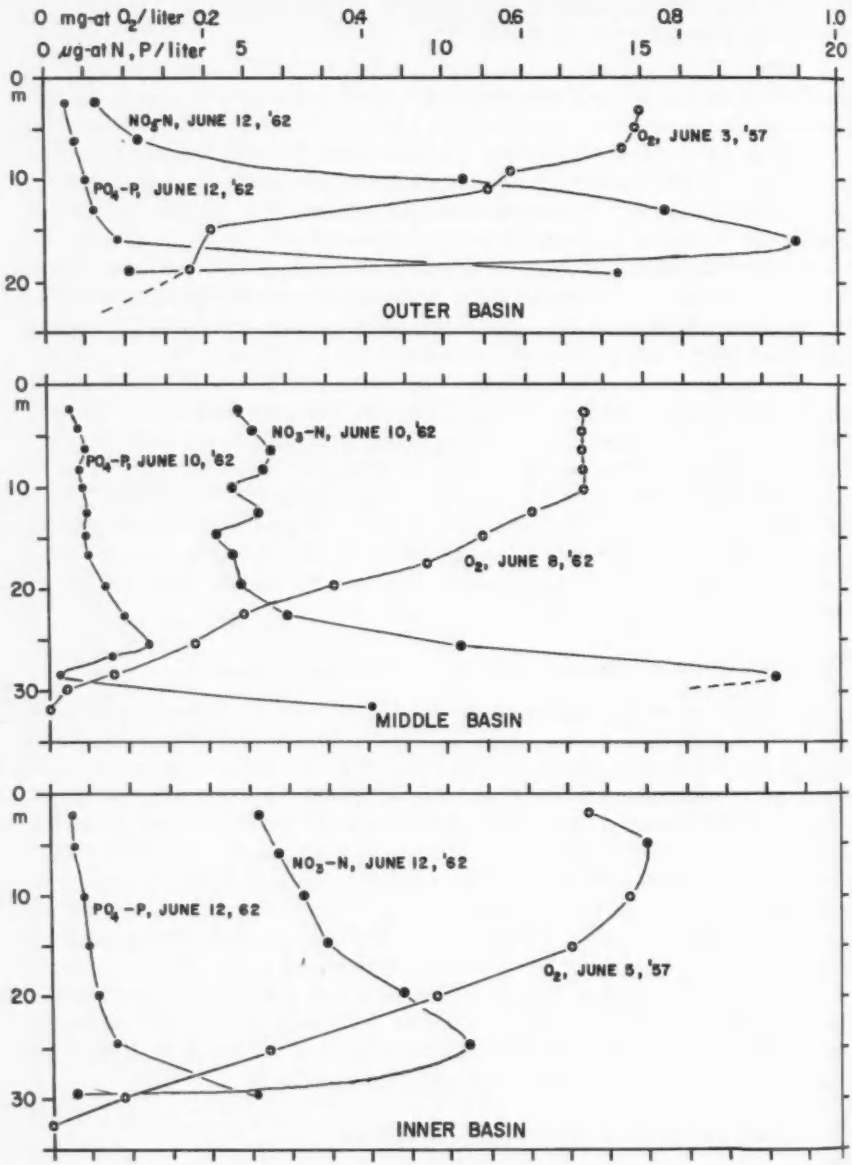

FIG. 20. Vertical distributions of PO_4–P and NO_3–N (plus NO–$_2$N) in relation to oxygen in the three basins of Ogac Lake.

apparent enrichment of water within a half meter of the bottom, even where the bottom was anoxic. The nitrate values were very low in the sediments, but again there was no enrichment of the bottom water. Evidence has been given

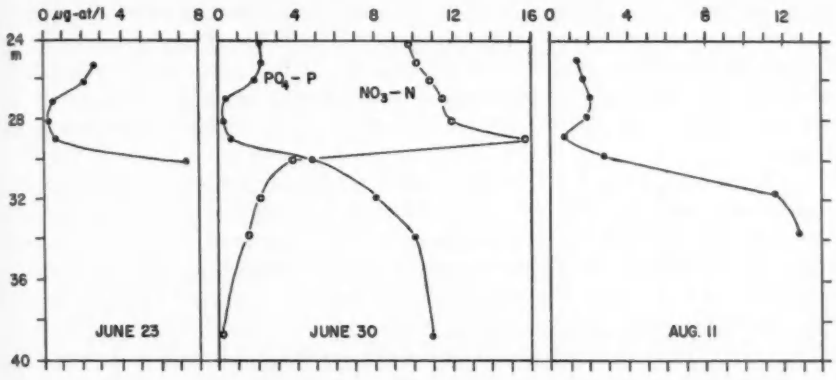

FIG. 21. Vertical distributions of PO_4–P and NO_3–N (plus NO_2–N) near the anoxic boundary in the middle basin of Ogac Lake in 1962.

(see section under heading Bottom Warming and Horizontal Heat Transfer) for restrictions on the lateral transport of heat away from the bottom and for the upward mixing of heat over the bottom. Therefore the lack of enrichments suggests that nutrients were not being gained from the sediments or, less likely, that nutrients were being biologically incorporated or degraded more rapidly over the bottom than at the same depths farther offshore. Nevertheless, differences in vertical distribution of nutrient levels in the three basins (Fig. 20) seem clearly related to morphometric differences (see Fig. 3), and the water column must be to some extent replenished by nutrients from the bottom at other times of year or over longer periods.

NUTRIENTS IN TIDAL WATER

Nutrients were measured in 1962 on three occasions in tidal water flowing into the lake. The results (µg-at/liter) were as follows.

Date	Size of Inflow (m^3)	PO_4–P	NO_3–N
June 20, PM	114,000	0.29	–
Aug. 17, PM	277,400	0.59	1.0
Aug. 18, AM	198,400	0.54	1.1

It is clear that the tides provide little inorganic nutrient, at least in summer when surface waters of the sea are exhausted of nutrients. However, the tides do supply much zooplankton and detritus, which may help maintain the general level of production in the lake in the face of presistent loss of nutrients to the depths.

COMPARISON WITH SIMILAR LAKES

Ogac Lake is at a particularly interesting stage in its isolation from the sea. Most other landlocked fiords that have been studied have permanent, if

very restricted, contact with the sea (Strøm, 1936; Northcote et al., 1964), or are dominated by fresh water (Murray and Pullar, 1910). Much of the unique hydrographic character of Ogac Lake derives from the combination of extremely large tidal amplitude and the narrow, steep-sided entrance from the sea. This is made clear from comparison with two similar lakes in northern Canada.

Carter (MS, 1963, 1965) has studied Tessiarsuk, a coastal meromictic lake in northern Labrador. This lake is much larger than Ogac Lake (545 vs. 148 ha) and tides of a given height above the lake displace proportionately less water (Fig. 22). Because of the smaller amplitude of tides (maximum range ca. 2.7 m), they rise, at most, about 60 cm above the level of Tessiarsuk, but enter the lake approximately 2 days out of 3, compared with about 1 day out of 5 at Ogac Lake. The final result, according to Carter (MS, 1963), is that Tessiarsuk, like Ogac Lake (see last paragraph in section Amount of Inflow), receives about one-quarter its volume in tidal water during the open-water season, but the quality of the inflow is very different. Because they do not rise as high above

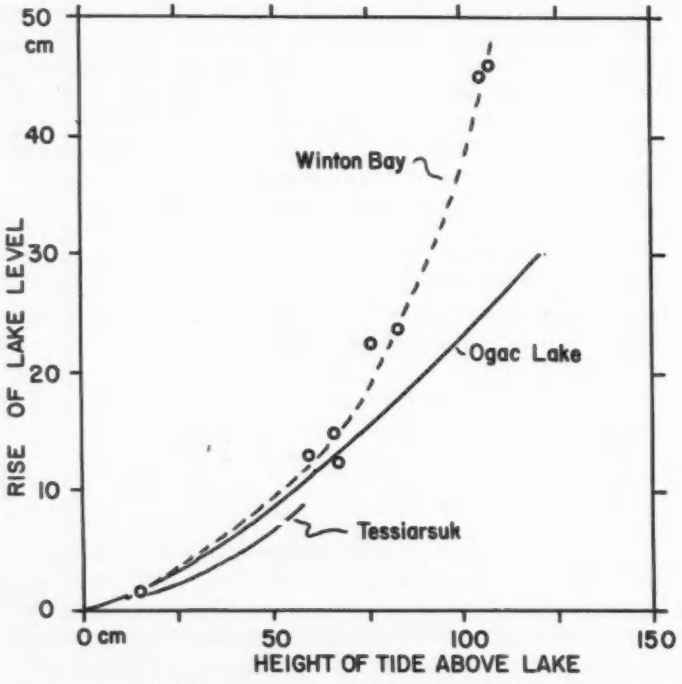

FIG. 22. Relationship between rise of lake level and height of tide above lake level for three semi-landlocked fiords or bays in northern Canada. The curve for Ogac Lake is from Fig. 4, that for Tessiarsuk is from Carter (MS, 1963), and points for Winton Bay are from observations at the inlet at high slack water in August 1962.

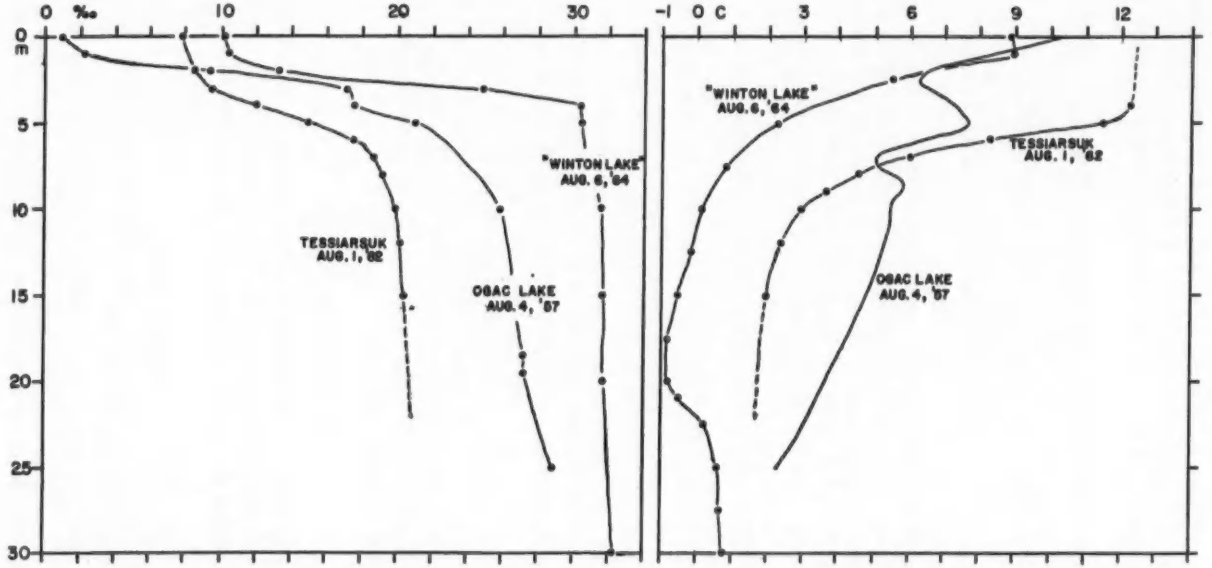

FIG. 23. Salinities and temperatures of the outer basins of three semi-landlocked fiords or bays in northern Canada. See text.

the lake, average tides at Tessiarsuk send in more water from near the surface of the sea. Further, because highest tides spill into Tessiarsuk across wide flats outside the main channel, they mix more with the fresh surface water of the lake. For both reasons, Tessiarsuk is replenished with less saline water than is Ogac Lake.

Observations were made by the present author at the semi-landlocked head of Winton Bay, southeast Baffin Island (63°24'N, 64°39'W), in August 1964. The highest tides observed at "Winton Lake" were about 1.1 m above lake level, similar to those at Ogac Lake. However, the range of tides at "Winton Lake" (maximum 7.5 m, determined from tide tables for nearby Brevoort Harbour) is smaller, and full-moon tides as well as new-moon tides entered the lake. "Winton Lake" therefore probably receives about twice as many tides as Ogac Lake. The replenishment effect of small tides (Fig. 22) is about the same in both lakes, although "Winton Lake" is larger (ca. 250 vs. 148 ha). The entrance to "Winton Lake" is not steepsided, and several other channels are flooded by the highest tides, which bring in much more water than the equivalent tides at Ogac Lake. In summary, "Winton Lake" receives proportionately much more seawater than Ogac Lake, and this water averages colder and more saline.

The effects of these tidal differences on the basic character of the three lakes is clear on Fig. 23. Tessiarsuk is considerably fresher than Ogac Lake, whereas the depths of "Winton Lake" are almost as salt as the sea outside. Differences in temperature are only partly due to tides. The Secchi disc depth at "Winton Lake" on August 6, 1964, was 17.5 m; this implies (Strickland, 1958) a vertical extinction coefficient of 0.1, close to that estimated for the upper waters of Ogac Lake (see Fig. 10). In Tessiarsuk (Carter, MS, 1963) the mean of five Secchi disc readings between August 1 and 16 was 6.8 $\pm$ 0.5 (95% f.l.), indicating a much larger extinction coefficient of about 0.25. Thus, Tessiarsuk and "Winton Lake" are relatively cold in the depths — the former because it accumulates little radiant heat, and the latter because of greater displacement rate by cold tidal water.

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In addition to those acknowledged for their assistance in the introductory paper (McLaren, 1967), I wish to thank my colleague Dr Bruno d'Anglejan for helpful discussion of certain physical and chemical problems.

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A Brief Survey of the Profundal Benthic Fauna of Lakes in Manitoba[1]

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ABSTRACT

The profundal benthic fauna of nine lakes lying along the margin of the Precambrian Shield in the Province of Manitoba was investigated during August 1963, and is described with particular attention to the midges (Diptera: Chironomidae).

Comparison with a Scottish lake, similarly situated with respect to Precambrian rocks, showed no close agreement in the distribution of species of Chironomidae. This can be credited to differences in the Palaeozoic rocks adjoining the Precambrian.

Chironomus tentans and *C. decorus* were most numerous and most frequent at water depths up to 15 m whereas *C. anthracinus* and *Chironomus* sp. A were generally in water over 20 m.

In Falcon, Reed, and Morton lakes, *C. anthracinus* tended to be more successful where sediments contained appreciable amounts of allochthonous debris and to give way to *Chironomus* sp. A where sediments were autochthonous.

INTRODUCTION

In Scotland and in Canada there are lakes sharing an unusual geographical feature in that they and their catchment areas lie partly on Precambrian and partly on Palaeozoic rocks.

The concept that such lakes in the two countries might have similar faunal distributions led to the survey which is the subject of this account. An additional incentive was the sparsity of published information on the nature and distribution of the invertebrate fauna of lakes in Manitoba and it was considered to be worthwhile adding to this despite the narrow spacial and temporal limits of a survey of the profundal bottom fauna confined to a single month (August 1963). The survey was principally a study of the distribution of larvae of chironomid midges. Other members of the macrofauna were recorded, mostly as classes or orders, for the purpose of comparing their biomasses within and between lakes at the time of collection.

In Scotland, the benthic fauna of the deep, fjord-like northern half of Loch Lomond, lying in a region of Precambrian (Dalradian) rocks, differs both qualitatively and quantitatively from that of the shallower, southern half which lies in a region of Devonian Old Red Sandstone largely overlain by glacial alluvium (Slack, 1965).

The lakes in Manitoba chosen for comparison (Fig. 1) were: Falcon Lake with West Hawk Lake and North Cross Lake as subsidiaries, in the Whiteshell region; Lake Winnipeg in the area between Berens River and Rabbit

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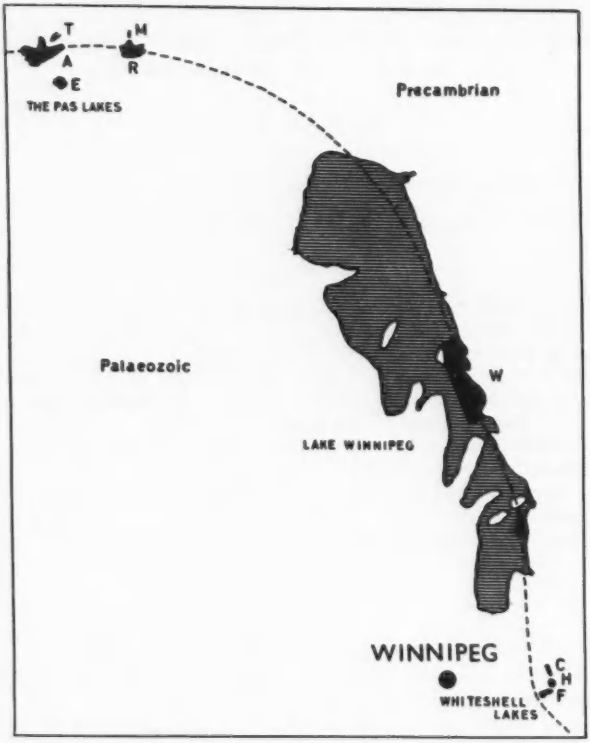

FIG. 1. The locations of the lakes with respect to the Precambrian Shield: F, Falcon Lake; H, West Hawk Lake; C, North Cross Lake; W, Lake Winnipeg; E, Egg Lake; A, Lake Athapapuskow; T, Twin Lake; R, Reed Lake; M, Morton Lake.

Point; Lake Athapapuskow with Twin and Egg lakes as subsidiaries and Reed Lake with Morton Lake as a subsidiary, these last five lakes being in the region of the Pas.

All lie along the margin of the Precambrian Shield, the principal lakes studied (Falcon, Winnipeg, Athapapuskow, and Reed) lying partly on the Archaean and partly on Palaeozoic rocks, while the subsidiary lakes are either on Archaean (Twin, Morton, and North Cross) or on Palaeozoic (Egg) (see Geological Map of Manitoba, Map 85 0A, Manitoba Department of Mines and Natural Resources, 1946).

Thus the four principal lakes fulfil the initial premise that they lie astride Precambrian and Palaeozoic ricks as does Loch Lomond. None shows any closer correspondence with that lake nor such a clear-cut division between the influences of old and younger rocks. This is due to the complexity of the latter and to the varying proportion of drainage areas on each in the Canadian lakes.

MATERIAL AND METHODS

Samples of approximately 0.1/m² areas were taken by Ekman grab. On Lake Winnipeg, where a 22-cm Ekman was used, two grabs constituted a sample. On all other lakes five grabs per sample were taken with a 15-cm Ekman. The reported quantities of animals captured in Lake Winnipeg have been adjusted to represent sampling areas equivalent to those of the other lakes.

Locations of the sampling stations are shown in Fig. 2 and 3. In the smaller lakes isolated loci were chosen in regions expected to give a general representation of the profundal bed. There were four such stations in Falcon Lake, two in Twin Lake, and single stations in all other subsidiary lakes.

More attention was paid to the larger lakes. In the Berens River area of Lake Winnipeg, stations were located along five transects (1W, 2W, 3W, 4W, 5W) crossing, as far as could be judged, the boundary of Precambrian

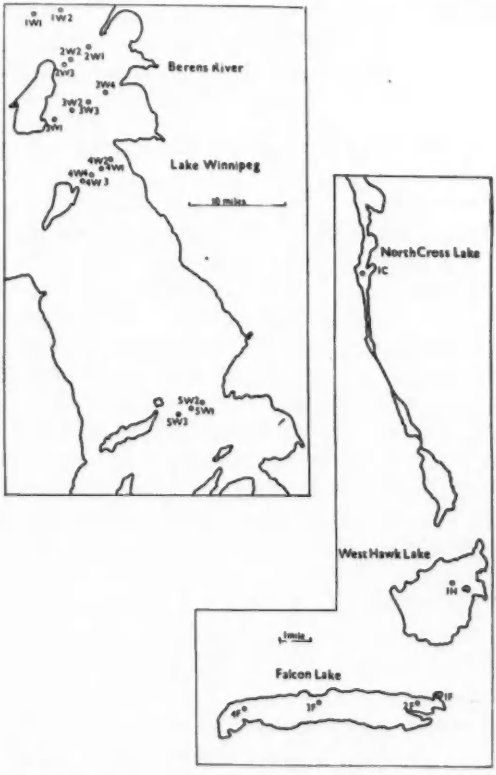

FIG. 2. The locations of the sampling stations in Lake Winnipeg and the Whiteshell lakes.

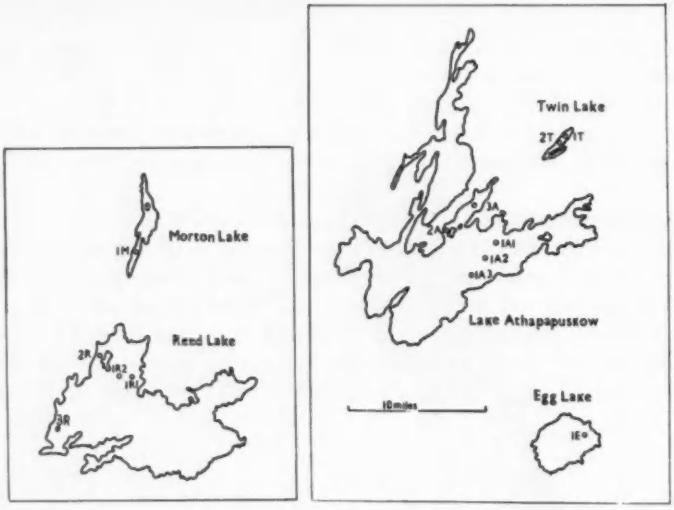

FIG. 3. The locations of the sampling stations in the Pas lakes.

rocks, and this method was also employed, though less extensively, in lakes Athapapuskow and Reed.

The samples were sieved through 70-mesh (0.2-mm aperture) fabric and the residues packed for transport in approximately 10% commercial formol. Since the formol was unneutralised and samples were unwittingly frozen on board ship during transfer to Scotland, molluscs and oligochaetes, but not the other groups, were insufficiently preserved for identification to species.

In addition to counts, volumes of the component animals were determined by a displacement method (see Appendix 3) as a measure of total biomass at each station and also for use in computing proportional composition.

The bottom deposits sampled are described from brief notes of physical appearance made in the field and microscopic examination of the sieve-residues. As a rough guide to the amount of organic debris in each sample, volumes of residues were recorded as percentages of total sample volumes. It must be noted, however, that where coarse sand having grain sizes greater than 0.2 mm occurred, this too was included in the residue volume. These data for each station are listed in Appendix 1.

RESULTS

Apart from that of Lake Winnipeg, the fauna comprised Nematoda, Oligochaeta, *Pontoporeia affinis* Lindstrom (Crustacea), Chironomidae and *Chaoborus* (Diptera), and Sphaeriidae (Mollusca) with a few occurrences of *Mysis relicta* Loven (Crustacea), Ceratopogonidae (Diptera), gastropod molluscs, and Hydracarina.

The Berens River region of Lake Winnipeg differed from all other lakes in the constant presence of *Hexagenia* sp. (Ephemeroptera) (it only occurred elsewhere at one station in Reed Lake) and Hirudinea with occasional specimens of the conchostracan *Leptestheria compleximannus* (Packard) (no leeches or Conchostraca were found elsewhere). *Chaoborus*, on the other hand, was absent although present in samples from all other lakes except Twin Lake.

Quantitative Notes on the Benthic Fauna

THE WHITESHELL LAKES

Falcon Lake.—In terms of volume, Chironomidae formed 52%, *Chaoborus* 32%, *Pontoporeia* 13%, and Oligochaeta and Mollusca 3% of the fauna in the samples. There were marked differences between the stations. *Chaoborus* was the highest in volume (82%) in the highly organic ooze of station 1F, Chironomidae dominated stations 2F and 3F, *Pontoporeia*, *Chaoborus*, and Chironomidae were equal in volume at station 4F. Oligochaetes and molluscs were poorly represented at all stations, nowhere exceeding 5% of all animals.

At the single stations of the subsidiary North Cross and West Hawk lakes, Chironomidae, *Chaoborus*, and tubificid worms were the principal animals in the first and *Pontoporeia* in the second.

Lake Winnipeg (The Berens River Region).—*Pontoporeia* and *Hexagenia* made up 35.8 and 33.4%, respectively, of the volume of the total fauna. These were followed by Mollusca and Chironomidae with 10.3 and 9.4%, the remainder being Oligochaeta and Hirudinea.

Lake Winnipeg being much larger than the other lakes studied, quantities per square meter have been estimated for whole transects instead of for individual stations. This has been done to make the distribution of faunal elements more readily appreciable over the comparatively large area studied.

A noticeable feature of the area as a whole was the uniformity of biomass (Fig. 4). Transect 3W produced considerably more than the others (22 ml/m^2), perhaps because the shallower water here favoured *Hexagenia*, but all the other transects only ranged from 14.3 to 17.0 ml/m^2 despite the fact that the component animals fluctuated markedly in relative abundance between one transect and another. For example, transect 4W had 48.4% *Pontoporeia* and 26.7% *Hexagenia* with 2.9% Oligochaeta and 4.4% Mollusca. Transect 1W had only 13.4% *Pontoporeia* and 10.3% *Hexagenia* whereas Mollusca and Oligochaeta increased to 29.0% and 35.8%. Yet the total biomasses differed only by 0.5 ml/m^2. Transects 2W and 5W showed a similar complementary representation of *Pontoporeia* and *Hexagenia*, the first having 55.4% and 18.8%; the second 16.9% and 70.4% with a biomass difference of 1.3 ml (Fig. 4).

THE PAS LAKES

All these more northern lakes yielded much lower quantities of animals than did Lake Winnipeg or Falcon Lake.

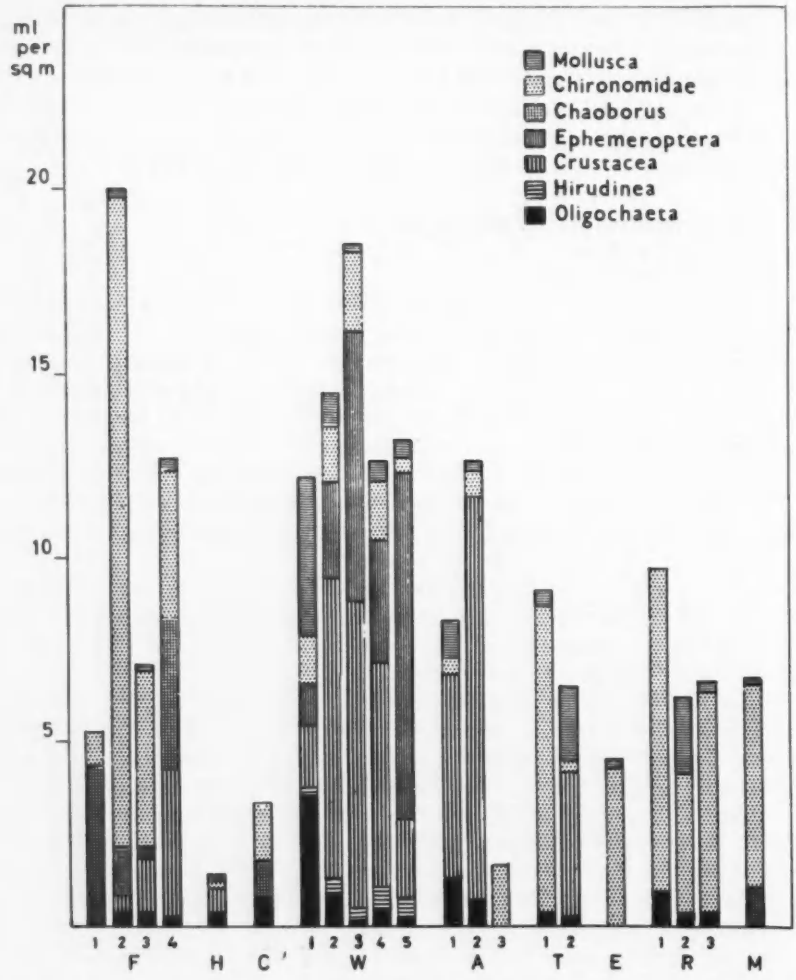

FIG. 4. Biomasses in millilitres per square metre along transects and at single stations. Letter code for lakes as in Fig. 1.

Lake Athapapuskow.—In this lake 52.3% of the volume of the fauna consisted of *Pontoporeia* and 37.1% of Chironomidae, with Oligochaeta and Mollusca forming the remainder.

Average values, however, are misleading. There were no animals other than Chironomidae at one station (3A) and the high percentage of these is largely due to their volume at this station. At all other stations, *Pontoporeia* predominated, the rest of the fauna being fairly equally divided among the other groups.

The fauna at the single station in Egg Lake was made up almost entirely of Chironomidae. In Twin Lake the first station had little other than Chironomidae and the second little other than *Pontoporeia* and Sphaeriidae.

Reed Lake.—Here the Chironomidae were highly predominant (82% of the volume) and *Pontoporeia* did not occur. A few specimens of *Chaoborus* were found at station 2R and in all samples the Oligochaeta failed to reach 10%. Stations 2R and 3R showed complementary distribution similar to that found in Lake Winnipeg. Although the difference in total biomass between 2R and 3R was only 0.3 ml/m², 2R had 61.6% Chironomidae and 33.6% Sphaeriidae while at 3R the values for these groups were 94 and 3.1%.

The single station in Morton Lake resembled Reed Lake in biomass and in the predominance of chironomids (.3%) but here oligochaetes were absent, there were few Sphaeriidae, and *Chaoborus* amounted to 15%.

Distribution of the Chironomidae

The impossibility of accurately determining larval Chironomidae to species without confirmation by rearing is very well known to all who have studied the freshwater benthos. At best they can be identified to species groups or, if to species, then only tentatively and with the reservation that the larval name may not agree with the imaginal. In this account, the authors principally consulted were Roback (1957), Curry (1958, MS, 1962), and Chernovskii (1949) and in the list given (Appendix 2) the author used is quoted after each larval form with a few exceptions. The particularly difficult Orthocladiinae were left as the subfamily and the four forms numbered. *Phaenopsectra* (*Sergentia*), which keyed to *Phaenopsectra* (*Sergentia*) *longiventris* group, agreed with the author's confirmed specimens of *Phaenopsectra* (*Sergentia*) *coracinus* and was considered to be that species.

Chironomus sensu stricto is a notoriously difficult genus with which to deal systematically in the larval state. Using the keys of Curry's recent work on the subgenus (Curry, MS, 1962), and my own confirmed specimens, four forms were recognised. Two in the "plumosus" group were identified as *C. tentans* and *C. decorus*. Of the other two, both in the "thummi" group, one so closely resembled confirmed larval specimens of *C. anthracinus* as to warrant the use of that name with equal validity. The other was clearly a different larval form although similar in some respects to *C. anthracinus*. Since it could not be keyed to a specific name it has been designated *Chironomus* sp. A to give it identity for discussion. These names, however, should still be regarded more as labels to distinguish one form from another than as identities in view of the uncertainty and confusion which exists in the identification of both larvae and imagines of species of *Chironomus* (Andersen, 1949; Acton, 1955).

Altogether 32 larval forms (see Appendix 2) were recognised but it must be emphasised that a collection made during August would be likely to represent only part of the chironomid fauna due to the emergence of many species and either the absence of their larvae from the profundal zone or their presence as early instars with identities too uncertain to justify inclusion.

Disregarding single specimens and occurrences comprising less than 10% of the number of all larvae at any one station, 16 larval forms were present in sufficient abundance as to be considered characteristic of their environments. These are: *Procladius* spp., *Pentaneura carnea*, Orthocladiinae sp. 2, Orthocladiinae sp. 3, Orthocladiinae sp. 4, *Protanypus* sp., *Prodiamesa bathyphila*, *Cryptochironomus digitatus*, *Phaenopsectra* (*Sergentia*) *coracinus*, *Harnischia amachaerus*, *Chironomus tentans*, *C. decorus*, *C. anthracinus*, *Chironomus* sp. A, and *Micropsectra* sp. 1.

DISTRIBUTION IN THE LAKES

Falcon Lake.—Six forms comprised more than 10% of all larvae: *Procladius* spp. at all stations, *Phaenopsectra* (*Sergentia*) *coracinus* at stations 3F and 4F, *Chironomus* sp. A at station 2F, *Chironomus anthracinus* at station 3F, *C. decorus* at station 1F, and *Micropsectra* sp. 1 at station 4F. *Procladius* spp. being active swimmers and largely carnivorous in habit, are governed more by food requirements than by kind of bottom sediment and therefore are generally distributed. *Phaenopsectra* (*Sergentia*) *coracinus* was present only in those sediments containing allochthonous wood fragments and this agrees with findings elsewhere (Slack, 1965; Lenz, 1928). *Chironomous* sp. A predominated in autochthonous sediments of the deep water of station 2F, *Chironomous decorus* in a similar sediment in shallow water, *C. anthracinus* in deep water and partly allochthonous sediment, and *Micropsectra* sp. 1 in water of intermediate depth but with a firmer sandy bottom.

West Hawk Lake.—The deep depression of this lake held only one species, Orthocladinae sp. 2. This limitation to an orthocladiinid species suggests marked oligotrophic conditions and absence of large oxygen deficits, the characteristic requirements of this subfamily.

North Cross Lake.—The markedly organic autochthonous sediment at the one station here yielded only six larvae but they were characteristic of the environment, viz.: four *Procladius* sp., one *Chironomus tentans*, and one *C. anthracinus*.

Lake Winnipeg.—Five representative forms occurred, four of them on all transects. *Procladius* spp. were generally distributed. *Pentaneura carnea*, another of the carnivorous Tanypodinae, exceeded 10% of the number of all larvae at stations along transects 2W, 4W, and 5W, and did not appear in any other lake except for a few specimens in Reed Lake. *Cryptochironomus digitatus*, present on all transects, exceeded 10% at 2W and 5W in the deeper water of each transect. Like *P. carnea* it was not found elsewhere except for a single specimen in Falcon Lake. *Chironomus tentans* larvae reached 30% on transect 1W, but elsewhere ranged only from 3 to 7% representation. They were all large though not clearly penultimate and emergence may well have been taking place. A number of *C. plumosus* imagines were collected in the area at the same time so that identity with this species is probable. The larvae considered to be *C. decorus*, on the other hand, were all in the first or second instars and consequently even less reliable material for identification. Apart

from the dubiety of calling these *C. decorus* it is probable that they comprised a mixture of species. They had a high representation on transects 2 to 5W, and "plumosus" group larvae as a whole comprised 30–40% of all chironomids. This uniformity of representation reflects the general uniformity of the bottom deposits. A milieu conferring an advantage on species of the "*plumosus*" or "*thummi*" groups would be a eutrophic mud, associated with a marked reduction of oxygen during periods of thermal stratification. In the region surveyed the muds were highly allochthonous and under the influence of the dystrophic Berens River (Bajkov, 1930), at variance with conditions in the main body of the lake. This difference, however, is almost certainly more apparent than real for there would be enrichment by drift into the area of much autochthonous debris.

Lake Athapapuskow.—There were clear regional divisions both between the transect in the open lake and the sheltered stations behind the island chain and between these two single stations.

On the transect the chironomids were Orthocladiinae (Orthocladinnae sp. 3 and Orthocladiinae sp. 4) and Diamesinae (*Protanypus* sp. and *Prodiamesa bathyphila*). At the single stations they were Chironominae, station 2A, in deep water and a very sandy deposit, was tenanted by *Micropsectra* sp. 1 and *Chironomus* sp. A; station 3A by *Chironomus tentans* in shallower water and a soft organic ooze. *Procladius* occurred but was scarcer than in any of the other lakes and did not attain a value of 10%.

Twin Lake.—Here also there was a marked difference between the stations. Both were in deep water but with different sediments. Station 1T had a large population solely of *Chironomus* sp. A in a soft organic sediment. Station 2T held *Phaenopsectra* (*Sergentia*) *coracinus* and *Micropsectra* sp. 1 in a coarser but firmer deposit by virtue of the numerous iron concretions.

Egg Lake.—This lake was sampled to provide a shallow, more eutrophic environment for comparison with Twin Lake but the samples only yielded eight specimens: four *Chironomus tentans*, two *Procladius*, and single specimens of *Chironomus* sp. A and *C. anthracinus*.

Reed Lake.—Four types characterised the profundal bed and, as in Lake Winnipeg, lack of variety in bottom deposits was reflected in the uniformity of chironomid species.

Transect 1R and station 2R were occupied principally by *Chironomus* sp. A and *Chironomus anthracinus* but at Station 3R, while these species were also present, *C. anthracinus* was largely replaced by *C. tentans*. Comparing the distribution with water depth, *Chironomus* sp. A fell from 85 to 23% of all larvae present as the depth decreased from 30 to 13 m. *Chironomus anthracinus* predominated at 13 m and gave place to *C. tentans* at 7 m. *Procladius* only exceeded 10% at station 3R.

Morton Lake.—Morton Lake resembled Reed Lake in having *Chironomus* sp. A., *Chironomus tentans*, and *C. anthracinus* with a predominance of *C. tentans*, a lower percentage of *C. anthracinus*, and relatively few *Chironomus*

sp. A. Here the bed was not unlike that at the Reed Lake profundal stations and the water depth only 10 m, suggesting a favouring of *C. tentans*.

DISCUSSION

In venturing to present the results of this survey as showing the distribution in kind and quantity of the profundal fauna of Manitoban lakes the limitations of the investigation must again be emphasised.

In the first place, the number of sites sampled was small and, in the second, samples taken on single visits during the month of August would yield only a part of the full insect complement. Nevertheless, certain features have emerged which can be discussed with the proviso that they need substantiating by further collections.

Biomass

Taking the fauna as a whole, the volumes of animals collected in lakes sampled at more than one site were converted to their equivalent dry weights by means of factors derived from measurements of similar fresh material. The dry weights, their standard deviations, and the numbers of individual grab-samples on which they depended were:

Lake	Dry weight of benthic animals (*kg/ha*)	Number of grab-samples
Winnipeg	31.2±12.5	29
Falcon	3.6± 1.5	29
Athapapuskow	3.4± 1.4	25
Twin	3.6± 0.9	9
Reed	2.4± 1.0	20

Rawson (1960) gives average values for benthic animals in 12 lakes in Saskatchewan. For five lakes lying wholly on the Precambrian Shield the mean value given is 2.8±1.3 kg/ha, for two lakes (Lac la Ronge and Lake Amisk) partly on the Shield it is 9.0±0.1 kg/ha, and for five lakes off the Shield it is 29.6±22.7 kg/ha.

With the exception of Lake Winnipeg, the results from the Manitoba lakes are akin to those from Saskatchewan lakes lying on the Precambrian Shield although of the former only Twin Lake lies wholly on it. The figure given for Lac la Ronge, however, applies only to the open water of the lake. In the island-studded northern half lying on the Shield the mean value for the same period was 2.8 kg/ha (Oliver, 1960).

So far as the small number of samples and brief period of collection can show, therefore, Winnipeg is the only lake in this account which demonstrates the effect of the Palaeozoic rocks bordering the Precambrian. This lake is exceptional among large lakes in having a low mean depth (13 m) and most

of its profundal zone is a suitable habitat for the large mayfly, *Hexagenia*. *Hexagenia* and the amphipod *Pontoporeia* accounted for 37 and 42% of the estimated dry weight, respectively. The remaining fauna averaged 6.4 kg/ha but with a standard deviation of 5.0 emphasising variability in abundance of the other groups of animals.

Bajkov (1930) has described the bottom fauna of Lake Winnipeg and given dry weights of collections from whitefish grounds which were not in the Berens River area. They yield the even higher value of 44 kg/ha so that my estimate of 31.2 kg/ha may possibly be indicative of a lowering of biomass by the dystrophic sediments brought into the area by the Berens River flowing off the Shield.

As has been pointed out by Larkin (1964), the genus *Pontoporeia* is a dominant element in the benthic fauna of Canadian lakes and in these results it comprised 56% of the average dry weight in Lake Athapapuskow and 34% of that of Twin Lake but only 15% in Falcon Lake and it played no part in that of Reed Lake.

Although there are no profundal amphipods in British lakes, Loch Lomond, sampled over a period of 2 years, yielded an average dry weight of benthic animal of 8.0 kg/ha (Slack, 1965). Loch Lomond thus resembles the southern half of Lac la Ronge where too the bulk of the fauna consists of chironomid larvae (Oliver, 1960).

The concept of spatial and temporal uniformity of biomass in a uniform environment has been put forward by other authors (Adamstone, 1924; Fedoruk, MS, 1964). The results from Lake Winnipeg and perhaps from Reed Lake (Fig. 4) uphold this concept in the low range of total biomass over the transects with widely different percentage composition of animal groups between them.

This difference of composition is more marked by a comparison of volumes than by a comparison of dry weights, suggesting that uniformity of total biomass is governed less by the amount of living material the environment can support than by other factors, such as living space required by each individual.

Chironomidae

The nine lakes in Manitoba have a geological location similar to that of Loch Lomond in that they lie along the margin of a Precambrian formation. In the Scottish lake a consequence of this is that there are only two main types of profundal bottom deposit: a soft, largely allochthonous and dystrophic ooze in the northern Precambrian region and a firmer, more autochthonous, substrate in the southern Devonian (Old Red Sandstone) region. The influence of the Devonian rocks, however, is not sufficient to advance the oligotrophic regime imposed by the Precambrian catchment area towards eutrophy to any marked degree in the southern area.

In the Manitoba lakes Palaeozoic limestones adjoining the Precambrian have enriched the waters and advanced eutrophication to a greater degree than that of Loch Lomond. This difference is shown by the benthic fauna in

the prevalence of species of *Chironomus* in the Canadian lakes as compared with Loch Lomond where the genus is represented by one species localised to one small area.

In Loch Lomond *Phaenopsectra* (*Sergentia*) *coracinus* is the predominant chironomid in the Precambrian region and it is absent from the Devonian region where *Tanytarsus* spp. and *Polypedilum convictus* group take its place (Slack, 1965). *Phaenopsectra coracinus* is a eurybathic, somewhat stenothermic species which appears to prefer an organic ooze having a large component of allochthonous material, particularly debris from trees. In the Manitoba lakes it was found in Falcon Lake and Twin Lake and these two showed the nearest approach to the environmental conditions of the Scottish lake. *Phaenopsectra coracinus* reached appreciable numbers in Falcon Lake at two stations where the substrate satisfied the above conditions but it did so in the presence of a larger population of *Chironomus anthracinus*. Both species were replaced in the firmer sandy muds of shallower water by Tanytarsinae, species of *Micropsectra*.

In Twin Lake *P. coracinus* and *Micropsectra* sp. 1 shared a sediment which had all the elements of marked dystrophy. The sieved debris was mainly an amorphous floc rendered coarsely particulate by iron concretions and appeared to be atypical for *P. coracinus* in the physical form of organic material present.

One other observation concerning the Chironomidae arising from the survey deserves mention. This was the apparent association of different species of *Chironomus* with water depth and type of bottom deposit.

Chironomus tentans and *C. decorus* were most frequent and most numerous in depths up to 15 m whereas *C. anthracinus* and *Chironomus* sp. A were generally in water deeper than 20 m. Both the last two occupied similar habitats but where they were the characteristic species (in Falcon, Reed, and Morton lakes) their population densities tended to be complementary. *Chironomus anthracinus* was the more abundant species where sediments contained appreciable amounts of allochthonous debris and it gave way to *Chironomus* sp. A in those with only autochthonous materials.

It must be fully realised, however, that apparent correlation with depth of water is an observation applicable only to this survey and that its validity even for these lakes requires substantiation by further investigation. It must certainly not be taken to have general application. For example. *C. anthracinus* inhabits Loch Lomond at about 10 m in the one small area where the bed is sufficiently eutrophic for it, whereas in Esrom Lake it dominates the profundal fauna at a depth of 21 m (Jónasson, 1961). The influence of depth on settlement of grades and types of sediment, on temperature and on oxygen deficits is the operative factor and these can be controlled in other ways.

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(Appendices 1–3 *follow*)

APPENDIX 1. Physical appearance of sediments and their sieve-residues at the collecting stations and macrofaunal biomasses.

Station	Water depth (*m*)	Type of sediment	Percentage volume and type of residue	Biomass (ml/m^2)
Falcon Lake				
1F	7.5	Fluid dark brown ooze.	4.4. Autochthonous faecal pellets and plankton chitin.	7
2F	21	Brown ooze, less fluid than at 1F.	0.7. Similar to 1F but with more plankton chitin.	20
3F	25	Similar to that at 2F.	0.8. Partly allochthonous wood fragments, faecal pellets, and plankton chitin.	7
4F	13.5	Soft sandy mud.	0.8. Similar to 3F.	12
West Hawk Lake				
1H	112.5	Black-brown ooze with a marsh odour.	0.9. Predominantly faecal pellets and plankton chitin but partly allochthonous wood fragments.	1
North Cross Lake				
1C	6	Soft brown mud with a strong bog odour.	1.0. Autochthonous plankton chitin.	3
Lake Winnipeg				
1W1	15	A uniform light brown mud with clayey plasticity.	0.9. Allochthonous moss and wood fragments.	14
1W2	15	As for 1W1.	0.8. As for 1W1.	10
2W1	9	Coarse sandy mud.	18.3. Sand and allochthonous wood fragments.	10
2W2	26	Light brown sandy clay.	3.2. Sand and allochthonous wood fragments.	8
2W3	26	As for 2W2.	1.1. Wood fragments.	24
3W1	7.5	Uniform light brown mud with clayey plasticity.	9.1. Allochthonous moss and wood fragments.	19
3W2	9	Uniform light brown mud with clayey plasticity.	3.3. Allochthonous moss leaves and wood fragments.	17
3W3	9	As for 3W2.	5.0. Wood fragments.	20
3W4	9	As for 3W2.	5.2. As for 3W3.	18
4W1	9	Firm sandy clay.	18.2. Sand, moss leaves, and wood fragments.	12

4W2	10	Soft sandy clay.	5.8. Sand and wood fragments.	14
4W3	13	Firm sandy clay.	3.0. As for 4W2.	9
4W4	17	As for 4W3.	9.1. Wood fragments.	17
5W1	7	Moderately firm clay.	12.3. Half faecal pellets, half wood fragments.	8
5W2	10	Soft dark brown clay-mud.	3.7 Wood fragments.	9
5W3	13	As for 5W2.	3.7. As for 5W2.	22
Lake Athapapuskow				
1A1	36	Sandy light grey-brown mud.	2.2. Sand and autochthonous alga (*Pithophora*) fragments.	10
1A2	33	As for 1A1.	0.5. Faecal pellets.	8
1A3	18	Firm light grey clay and small stones.	2.5. Sand and *Pithophora* fragments.	6
2A	21	Black-brown coarse sand.	6.2. Sand and faecal pellets.	13
3A	14.5	Soft brown ooze.	1.1. Faecal pellets.	3
Twin Lake				
1T	22	Soft sienna brown.	0.5. As for 3A.	9
2T	19	Ferruginous dark brown mud with numerous iron nodules.	2.3. Iron concretions and faecal pellets.	6
Egg Lake				
1E	11	Soft greenish-khaki chalky ooze.	1.8. Faecal pellets, oligochaete coccoons, and plankton chitin.	4
Reed Lake				
1R1	31	Light grey-brown mud.	0.2. Plankton chitin and faecal pellets with a low content of allochthonous wood fragments.	4
1R2	30	As for 1R1.	0.3. As for 1R1.	7
2R	13	Light grey-brown mud.	0.2. Plankton chitin and faecal pellets with more wood fragments than 1R.	9
3R	7.5	Khaki-brown mud.	0.4. As for 2R.	5
Morton Lake				
1M	9	Soft khaki-brown sandy mud.	1.5. Faecal pellets with a low content of wood fragments.	7

APPENDIX 2. Larval forms of Chironomidae collected with references to authors consulted for identification, and their occurrence in the lakes.

	Author	Lake[a]								
		F	C	H	W	A	T	E	R	M
Subfamily Tanypodinae										
Procladius spp.	Roback, 1957	+	+	−	+	+	+	+	+	+
Pentaneura carnea	" "	−	−	−	+	−	−	−	+	−
Pentaneura sp. e.	" "	−	−	−	+	−	−	−	−	−
P. lentiginosa group[b]	Lenz, 1936	−	−	−	−	+	−	−	−	−
Pelopia sp.[b]	Roback, 1957	+	−	−	−	−	−	−	−	−
Anatopynia sp.[b]	" "	−	−	−	−	−	−	−	+	−
Psectrotanypus brunnei	" "	+	−	−	−	−	−	−	−	−
Subfamily Orthocladiinae										
Orthocladiinae sp. 1		−	−	−	+	−	−	−	−	−
" sp. 2		−	−	+	−	+	−	−	−	−
" sp. 3		−	−	−	−	+	−	−	−	−
" sp. 4		−	−	−	−	+	−	−	−	−
Subfamily Diamesinae										
Protanypus morio	Roback, 1957	−	−	−	−	+	−	−	−	−
Prodiamesa bathyphila	" "	−	−	−	−	+	−	−	−	−
Subfamily Chironominae										
Cryptochiromonus digitatus	Curry, 1958	+	−	−	+	−	−	−	−	−
C. fulvus	" "	−	−	−	−	−	−	−	+	−
C. blarina	" "	−	−	−	−	−	−	−	+	−
Harnischia amachaeirus	Roback, 1957	−	−	−	+	−	−	−	−	−
Sergentia coracinus	" "	+	−	−	−	−	+	−	+	−
Polypedilum halterale	" "	−	−	−	−	−	−	−	+	−
Glyptotendipes senilis	" "	−	−	−	−	−	−	−	+	−
Microtendipes pedellus[b]	" "	−	−	−	−	−	−	−	+	−
Chironomus sp. A	" "	+	−	−	−	+	+	+	+	+
Chironomus tentans	Curry, 1962	+	+	−	+	+	−	+	+	+
C. decorus	" "	+	−	−	+	−	−	−	−	−
C. anthracinus	" "	+	−	−	−	−	−	+	+	+
Stictochironomus sp.	Roback, 1957	−	−	−	+	−	−	−	−	−
Tanytarsus gregarius gp.	Chernovskii, 1949	+	−	−	+	+	−	−	+	−
Atanytarsus sp.[b]	" "	−	−	−	−	−	−	−	+	−
Zavrellia sp.	" "	−	−	−	−	−	−	−	+	−
Micropsectra sp. 1	Roback, 1957 (genus)	+		−	−	+	−	−	−	−
Micropsectra sp. 2	Roback, 1957 (genus)	−	−	−	−	+	−	−	−	−

[a]Key to Lakes: F, Falcon Lake; C, North Cross Lake; H, West Hawk Lake; W, Lake Winnipeg; A, Lake Athapapuskow; T, Twin Lake; E, Egg Lake; R, Reed Lake; M, Morton Lake.
[b]Single specimens.

APPENDIX 3. Apparatus for the measurement of small volumes.

The apparatus (Fig. 5) used to determine volumes by displacement consists of a platform (A) capable of being raised or lowered by a fine-thread screw (B). Its vertical position is indicated on a dial (C) by a long arm (D) fixed to the axle of a pulley wheel (E), one of a pair placed

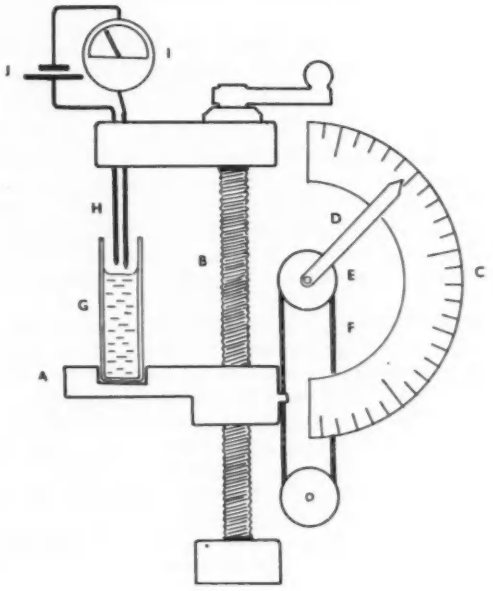

FIG. 5. Operational diagram of instrument for measuring small volumes.

above and below the platform and turned by a continuous band (F) attached to it. A small glass specimen tube (G), partly filled with 70% alcohol containing a trace of an electrolyte, is placed on the platform and the latter raised until the fluid just touches the tips of two platinum wires (H) vertically centered over the tube. The exact point of contact is facilitated by incorporating these wires in an electric circuit consisting of an ammeter (I) and battery (J). The fluid completes the circuit on touching and gives a reading on the ammeter. This first level (X) having been noted, material to be measured is drained on filter paper, the tube lowered, the material inserted in it, and the tube again raised into contact with the wires at a second level (Y). Level X – level Y gives a measure of the volume of the material the dial having been previously calibrated for any particular specimen tube by observing the displacement effected by small ball bearings of known volume. Volumes are determined to an accuracy of 0.01 ml.

Contributions of Year-Classes of Blue Pike to the Commercial Fishery of Lake Erie, 1943–59[1]

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ABSTRACT

The blue pike (*Stizostedion vitreum glaucum*) contributed about 12.7 million lb annually to the commercial production of fish in Lake Erie in 1915–59. Production averaged about 27% of the total for all species; in some years it exceeded 50%. The catch fluctuated greatly and was featured by a series of seven "highs" and "lows" during the 45-year period. The landings ranged between 2 million and 26 million lb; periods of peak production were 5 to 9 years apart. A sharp decline in the catch started in 1957. The take of 79,000 lb in 1959 was the lowest on record to that time.

Age and size compositions of the catch were determined from samples of blue pike taken from commercial landings in the fall, 1943–59. Peaks in production in that period were attributed to a few strong year-classes separated by several weak year-classes. Of the 20 year-classes represented in the samples, those of 1944 and 1949 were by far the strongest; together they contributed 42% (by weight) of the fall blue pike production in 1943–59. The strength of the 1939 and 1940 year-classes was moderate and the 1954 year-class was the last one of any importance. The other 15 year-classes were weak.

The 1957–59 decline in production was accompanied by a marked increase in rate of growth. Blue pike in age-group III weighed nearly eight times more and were 7.7 inches longer in 1959 than in 1951. Landings after 1958 consisted of only a few large fish. The collapse of the fishery forced blue pike fishermen either to fish for less valuable species or to discontinue operation.

INTRODUCTION

The blue pike (*Stizostedion vitreum glaucum*) has been a most important species in the commercial fishery of Lake Erie; it contributed more than one-fourth of the total catch in 1915–59. The blue pike was valued highly also as a sport fish; in some years, sport catches undoubtedly contributed substantially to the total production. However, changes in recent years have altered the situation entirely. Almost complete lack of recruitment led to record low production in 1958 and 1959. The blue pike fishery is temporarily, perhaps, permanently, in a state of collapse.

The habitat of the blue pike overlaps that of the related subspecies, the walleye (*Stizostedion vitreum vitreum*), in Lake Erie, but the areas of greatest abundance are different. The blue pike is most common in eastern Lake Erie where waters are cool and deep, whereas the walleye is most plentiful in the warm shallow waters of western Lake Erie. The two subspecies are readily separated on the basis of color — blue pike have no yellow pigment; their morphometric differences are too small to be useful for separation of the

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subspecies in the field (Deason, MS, 1936; Stone, MS, 1948). Growth rate was usually much slower in the blue pike than in the walleye (Adamstone, 1922; Deason, 1933).

The present paper is largely a statistical account of the changes in the blue pike fishery, with particular reference to the effects of the strength of various year-classes on the fall fishery. The possible effects of changing biological conditions in the lake on fluctuations in year-class strength are not discussed. Since the species composition of the commercial catches in Lake Erie has changed substantially over the years, it may be assumed that the biological character of the lake also is changing. Fishing methods, gear, and intensity have differed so little over the years in the U.S. waters of the lake that the fishery cannot be held directly accountable for the many changes in production and stocks.

Blue pike production in Lake Ontario, which averaged about 1% of that in Lake Erie, collapsed in 1956 — 2 years before the failure in Lake Erie.

MATERIALS AND METHODS

Scale Collections

Investigations of the contributions of year-classes of blue pike to the fall commercial catch were based on samples of scales and length and weight measurements from 8534 fish; 54 samples were taken from landings at several ports during the fall in 1943–57 (Table I). Samples were not recorded separately by port and gear in 1958 and 1959. Samples of 353 blue pike from Conneaut, Ohio, in April 1951, and 122 at Wheatley, Ontario, in April 1952 are not included in the table but are used for seasonal comparisons of age composition. Gear and numbers of samples taken were: trap nets, 27; gill nets, 26; and pound net, 1. About 50% of all samples were from Conneaut, Ohio, and Erie, Pennsylvania. Others were from Dunkirk, New York; Lorain, Vermilion, and Sandusky, Ohio; and Wheatley, Ontario (Fig. 1).

Trap nets used in Ohio waters had a crib of $2\frac{3}{4}$- to 3-inch mesh (extension measure). Gill-net samples of blue pike prior to 1957 were mostly from gear with meshes of approximately $2\frac{3}{4}$–3 inches, but in 1957–59 most fish, because of their large size, were caught in $4\frac{3}{4}$-inch mesh whitefish nets.

Size of samples and ports of origin varied considerably from year to year. Commercial landings usually were sampled only during a brief period in the fall. Differences in weather conditions and in availability of blue pike at the ports caused a wide variation in the size and geographical distribution of the annual samples.

Total length in inches and weight in ounces were measured for each fish. Scales were removed just above the lateral line below the spiny dorsal fin. Because most blue pike were sold in the round, the fish usually were not opened for determination of sex. All samples were from fish as landed. Undersized fish[2] were included when they occurred in some samples from Ohio because

[2]The minimum legal length for blue pike was 11 inches in Ohio throughout the period of collection; Pennsylvania and New York had no size limits.

TABLE I. Numbers of blue pike sampled from commercial landings, 1943–59.

Port and gear	Year															
	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	Total
Sandusky																
Trap net	–	–	–	117	199	250	–	–	–	166	144	–	–	150	–	1026
Wheatley																
Pound net	–	–	–	–	–	–	–	–	–	–	173	–	–	–	–	173
Gill net	–	–	–	–	–	–	–	–	–	–	–	119	120	157	–	396
Total	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	569
Lorain-Vermilion																
Trap net	122	–	–	–	–	–	160	–	–	–	–	127	104	–	–	513
Gill net	123	73	–	55	107	233	–	–	–	–	124	–	–	151	–	866
Total	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1379
Conneaut																
Trap net	208	85	–	166	342	197	180	136	214	174	–	–	155	156	–	2013
Gill net	–	–	179	–	–	–	–	–	–	–	–	–	–	–	–	179
Total	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2192
Erie																
Trap net	–	–	–	–	–	–	–	–	–	173	125	–	–	149	–	447
Gill net	252	106	221	–	150	233	181	122	–	–	–	147	147	150	128	1837
Total	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2284
Dunkirk																
Trap net	–	–	–	–	–	–	–	–	–	135	–	–	–	153	112	400
Gill net	–	–	–	–	–	–	–	135	–	–	142	50	140	–	–	467
Total	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	867
Grand total	705	264	400	338	798	913	521	393	214	648	708	443	666	1066	240	8534[a]

[a]Includes 108 fish sampled in 1958 and 109 in 1959 which were not separated according to port or gear.

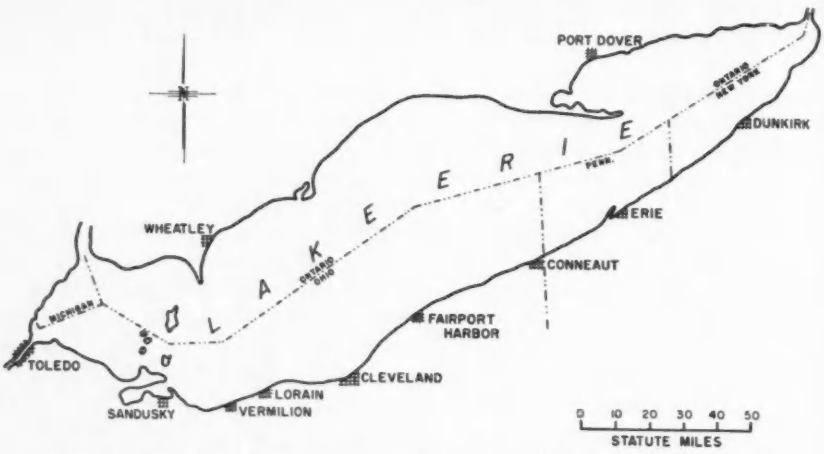

FIG. 1. Lake Erie, showing locations where commercial landings were sampled.

they normally were marketed. Ohio permitted the landing of limited quantities of undersized fish.

Ages were determined by counting the annuli on the scales. Although the scales taken in 1943–46 had been examined previously by Frank W. Jobes (Van Oosten, 1948), I read these same scales to ensure consistency of interpretation. The two sets of age determinations agreed closely. A thorough inquiry into the validity of the scale method for age determination of blue pike was not made, but Deason (1933; MS, 1936) presented strong supporting evidence. The validity of the scale method for the closely related walleye was established by Carlander (1945) and Hile (1954). In the present study the persistent strength or weakness of certain year-classes of blue pike in successive calendar years gives additional evidence that age determinations are generally accurate.

SOURCES OF STATISTICS

Production figures for blue pike given in this paper are from Baldwin and Saalfeld (1962) and start with 1915, the first year that the blue pike and walleye were separated in Canadian statistics. Ohio catches of blue pike by month and district and catch per unit of effort are from a summary of the Ohio commercial catch in Lake Erie for 1948–56 and from annual summaries in 1957–59 (Ohio Department of Natural Resources, MS, 1957; MS, 1958; MS, 1959).

PRODUCTION, FISHING INTENSITY, AND AVAILABILITY

PRODUCTION BY STATE AND PROVINCE, 1915–59

The blue pike has been a "money" fish in the Lake Erie fishery since earliest records. Large catches of blue pike were reported as early as 1850,

and in 1885 blue pike contributed about 8 million lb to the fishery (Smith and Snell, 1891).

Approximately 571 million lb of blue pike (26.6% of the total production of all species) were taken in the commercial fishery in Lake Erie by the United States and Canada in 1915–59 (Table II). Blue pike contributed more than 50% of the total catch in 1936, 1943, and 1944, and between 40 and 50% in 1930, 1937, and 1949.

The commercial catch of blue pike exhibited extreme fluctuations. Production from 1915 to 1957 included a series of highs and lows ranging between extremes of 26 million and 2 million lb, with peaks from 5 to 9 years apart (Fig. 2). The catch of 1,400,000 lb in 1958 was the lowest on record up to that time, and production in 1959 of only 79,000 lb marked the collapse of the fishery.[3]

Despite extreme fluctuations, total catches of blue pike showed no distinct trends except for the extremely sharp decline in production which began in 1958. Mean annual production in 1915–59 was 12,681,000 lb (Table III). The highest mean annual production for shorter periods was 16,575,000 lb in 1930–39 and the lowest was 8,761,000 lb in 1915–19. Despite the low production in 1958 and 1959, the average annual take for 1950–59 was only 1 million lb below the 45-year average.

Catches of blue pike in the United States and Canada, considered separately, have shown definite trends since 1915. Average annual U.S. production by periods increased from 6,529,000 lb in 1915–19 to 10,971,000 lb in 1930–39 and then decreased to 4,849,000 lb in 1950–59, whereas average annual Canadian production increased steadily (except in 1940-49) from 2,232,000 lb in 1915–19 to 6,958,000 lb in 1950–59. Much of the rise in Canadian production, particularly after 1949, was caused by increased fishing intensity. This increase was caused primarily by the introduction of nylon gill nets in 1949–50. The United States contributed 60 to 74% of the total blue pike production during the periods prior to 1950, but only 41% in 1950–59. The range of the percentage contribution of annual U.S. production to the lakewide total was 35 (1951) to 79 (1915); the 45-year average was 61.

The differences in trend make it difficult to judge the degree of similarity of short-term fluctuations in the production of blue pike in the U.S. and Canada. To permit better comparisons, trend lines were fitted to the production data for 1915–35 and 1936–56 in the U.S. and for 1915–56 in Canada. Deviations of the respective annual catches from the trend lines for the U.S. and Canadian production had a highly significant positive correlation ($r = 0.650$; $p = 0.001$; $df = 40$)—a strong indication that the U.S. and Canadian fishermen exploited common stocks of blue pike.

The percentage contributions of Ohio, Pennsylvania, and New York to the U.S. catch of blue pike have shown no clear trend (Table IV). The average percentages of U.S. production landed in these states in 1915–59 were Ohio,

[3]Annual catches in pounds of blue pike in Lake Erie in 1960–64 were: 1960—12,000; 1961—3000; 1962—1000; 1963—<500; 1964—<500.

TABLE II. Commercial production (thousands of pounds) of blue pike in Lake Erie, 1915–59.[a]

Year	United States				Canada: Ontario	Lake total
	Ohio	Pennsylvania	New York	Total		
1915	13,079	4,796	886	18,761	4,882	23,643
1916	7,683	1,408	298	9,381	2,539	11,920
1917	1,499	88	18	1,605	566	2,710
1918	1,069	79	75	1,222	785	2,007
1919	1,532	80	63	1,675	2,388	4,063
1920	3,494	302	169	3,965	3,355	7,319
1921	5,836	2,741	367	8,944	6,367	15,311
1922	7,202	2,593	565	10,359	6,313	16,672
1923	6,028	3,013	642	9,683	3,194	12,877
1924	5,363	3,077	527	8,967	2,988	11,955
1925	4,047	–	–	10,478	3,330	13,808
1926	4,234	2,936	2,170	9,340	2,975	12,315
1927	4,637	2,190	475	7,301	3,078	10,379
1928	3,743	627	449	4,819	2,104	6,923
1929	1,803	713	305	2,820	2,538	5,359
1930	9,017	2,211	564	11,792	5,898	17,691
1931	7,849	3,690	1,103	12,643	5,358	18,001
1932	7,784	1,607	475	9,867	3,962	13,829
1933	6,735	1,747	304	8,786	4,152	12,938
1934	5,765	2,132	459	8,356	2,298	10,654
1935	7,142	2,084	460	9,686	5,064	14,750
1936	16,447	2,837	624	19,909	6,879	26,788
1937	7,020	2,304	1,638	10,961	9,355	20,316
1938	6,154	1,442	1,064	8,659	7,158	15,817
1939	7,263	1,257	529	9,049	5,911	14,960
1940	4,541	313	97	4,951	2,012	6,963
1941	3,029	217	33	3,287	1,544	4,831
1942	5,296	824	98	6,222	4,405	10,627
1943	8,055	2,364	809	11,228	9,614	20,842
1944	11,278	2,129	1,526	14,933	9,390	24,323
1945	5,167	1,762	843	7,772	6,559	14,331
1946	2,550	351	111	3,012	1,909	4,921
1947	2,896	145	78	3,120	1,646	4,766
1948	6,957	1,473	553	9,003	5,742	14,745
1949	10,616	2,479	905	14,000	9,784	23,783
1950	4,900	1,112	178	6,190	8,611	14,801
1951	1,867	174	109	2,150	3,914	6,064
1952	5,531	1,081	158	6,771	7,267	14,038
1953	6,853	924	265	8,042	10,333	18,375
1954	4,576	1,349	319	6,245	8,151	14,396
1955	3,679	2,335	1,634	7,648	12,037	19,685
1956	4,703	1,231	921	6,855	12,002	18,857
1957	2,915	629	437	3,981	6,389	10,370
1958	366	74	136	576	824	1,399
1959	20	5	7	32	47	79

[a]Data are from Baldwin and Saalfeld (1962). Records are not available for production in Pennsylvania and New York in 1925. Michigan production (included in U.S. and Lake totals) was less than 500 pounds except for the following years: 1941—8000 lb; 1942—4000; 1946 and 1947—1000; and 1948—20,000.

69; Pennsylvania, 21; and New York, 10. Periods of highest mean annual production were Ohio, 8,118,000 lb in 1930–39; Pennsylvania, 2,219,000 lb in 1920–29; New York, 1,505,000 lb in 1940–49.

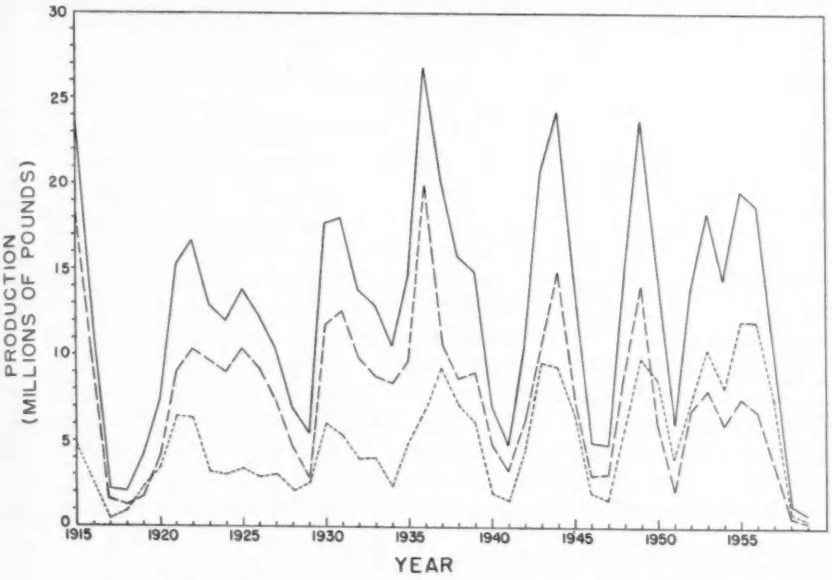

FIG. 2. Commercial production of blue pike in Lake Erie, 1915–59. Province of Ontario, short dashes; United States, long dashes; and Lake Erie total, solid line.

TABLE III. Average annual production (thousands of pounds) of blue pike in U.S. and Canadian waters of Lake Erie during different periods in 1915–59. (Percentages of total catch of blue pike in parentheses.)

Period	Number of years	United States	Canada	Total
1915–19	5	6,529 (74)	2,232 (26)	8,761
1920–29	10	7,668 (68)	3,624 (32)	11,292
1930–39	10	10,971 (66)	5,604 (34)	16,575
1940–49	10	7,753 (60)	5,261 (40)	13,014
1950–59	10	4,849 (41)	6,958 (59)	11,807
1915–59	45	7,667 (61)	5,014 (39)	12,681

The most productive blue pike fishery in the U.S. was in Ohio east of and including Fairport Harbor, where nearly 63% of the state's blue pike were produced in 1956–59. About 95% of the Ohio catch in 1948–59 was taken in

TABLE IV. Average annual production (thousands of pounds) of blue pike in Ohio, Pennsylvania, and New York and (in parentheses) percentage contributions of each to the U.S. total in Lake Erie during different periods in 1915–59.

Period	Number of years	Ohio	Pennsylvania	New York	Total[a]
1915–19	5	4,972	1,290	266	6,529
		(76)	(20)	(4)	
1920–29	10	4,639	2,219	810	7,668
		(60)	(29)	(11)	
1930–39	10	8,118	2,131	722	10,971
		(74)	(19)	(7)	
1940–49	10	6,039	1,206	505	7,753
		(78)	(16)	(6)	
1950–59	10	3,541	891	416	4,849
		(73)	(18)	(9)	
1915–59	45	5,516	1,576	575	7,667
		(69)	(21)	(10)	

[a]Includes Michigan catches, none of which exceeded 0.5% of the total catch in any period.

trap nets, and more than half (58%) of the U.S. production in the same years was in May and June, the spawning months for this species.

RELATION BETWEEN PRODUCTION AND AVAILABILITY

Knowledge of the general relation between production and the availability or abundance of blue pike in Lake Erie is most important to an understanding of data presented in later sections. Regrettably, useful statistics on catch per unit of effort are lacking for some waters of Lake Erie and are incomplete for others. The actual contributions of the year-classes to the commercial landings can be estimated with fair precision, but interpretation of these estimates in terms of year-class strength requires some assurance that fluctuations of catch and abundance are similar.

The continuing collection of catch-effort statistics was started in New York and Pennsylvania in 1950. Because of the changes in the blue pike population that began shortly after the middle of the decade, the period for which usable statistics are available is too short for a study of the relation between production and catch per unit of effort. The catch in gill nets (the dominant gear in these two states) was affected particularly by the increase in mesh size that accompanied the increase in size of blue pike.

The situation is considerably better in Ohio, where records of total effort and catch start with 1948. Helpful, also, is the fact that such a high proportion of the Ohio catch of blue pike was produced by trap nets, a gear little affected by changes in size composition. Further discussion in this section is based entirely, therefore, on the Ohio trap-net statistics.

The Ohio statistics have two shortcomings. The effort is in terms of the total number of trap nets lifted rather than the number of lifts in which blue pike were caught (the "effective fishing effort" described by Hile, 1962); and the recorded lifts are for all Ohio waters, although relatively few blue pike were taken in the westernmost of the three statistical districts, usually for only a short period in the fall. I believe, however, that neither defect is highly damaging. When blue pike were present in considerable numbers they were taken daily by trap netters in most of the central and all of the eastern district; thus the total fishing effort and the effective fishing effort for blue pike in these waters must have been nearly identical. The charging of fishing effort from the western district against blue pike does offer a source of bias, but estimates of fluctuations in availability would not be affected adversely unless the percentage of the total lifts made in the western district fluctuated substantially from year to year. I found no evidence of any great differences among the districts in the trends of fishing pressure and believe, therefore, that the catch per trap-net lift, computed from the total production of blue pike in trap nets and the total number of lifts in all Ohio waters, offers a reasonably dependable measure of annual fluctuations in the availability of blue pike in Ohio.

Fluctuations in the total production of blue pike in Ohio waters sometimes were greater than were those in the catch per trap-net lift but they agreed in showing a strong though irregular downward trend (Table V, Fig. 3). There is some evidence that the progressive downward shift in production may be attributed to the fairly consistent downward trend in fishing effort.

Despite certain disagreements between the curves of production and catch per unit of effort, either curve would have led to much the same conclusions regarding annual fluctuations in the abundance of blue pike. The

TABLE V. Production (thousands of pounds) of blue pike taken by trap nets, total number of trap-net lifts, and catch of blue pike per lift in Ohio waters of Lake Erie, 1948–58.

Year	Production	Number of lifts	Pounds per lift
1948	6,726	187,363	35.9
1949	10,259	169,006	60.7
1950	4,735	151,291	31.3
1951	1,817	144,180	12.6
1952	5,430	162,470	33.4
1953	6,435	136,629	47.1
1954	4,343	136,570	31.8
1955	3,423	106,956	32.0
1956	4,265	107,155	39.8
1957	2,611	110,620	23.6
1958	323	99,660	3.2

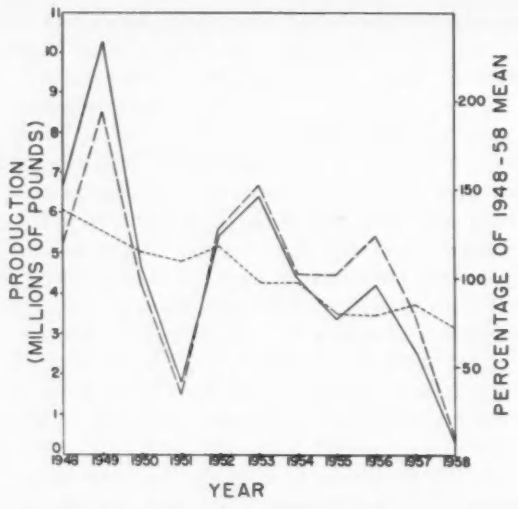

FIG. 3. Production of blue pike (solid line), fishing intensity (short dashes), and catch per trap net lift (long dashes) in the commercial trap-net fishery of the Ohio waters of Lake Erie, 1948–58. Scale at left applies to production only; scale at right applies to all three variables.

coefficient of correlation between the two sets of values was high ($r = 0.947$; $p = 0.001$; df = 9). It cannot be assumed that a similar relation between catch and availability existed in all blue pike fisheries, but the finding for the important trap-net fishery of Ohio lends confidence in the use of production statistics to judge changes of abundance in sections of Lake Erie where data on catch per unit of effort are not available.

That fluctuations of catch and availability of blue pike in the Ohio trap-net fishery are closely similar is in agreement with the opinions and findings of other investigators. Doan (1942) held that catch records for Lake Erie species, though not perfect measures, did reflect well all major changes of abundance. He reproduced figures from Hile (1937) in support of his view that catch and catch per unit of effort were correlated closely. A similar observation was made by Van Oosten et al. (1946).

AGE COMPOSITIONS, LENGTHS, AND WEIGHTS

VARIABILITY OF SAMPLES BY PORT, SECTION OF LAKE, AND GEAR

A study of the contributions of year-classes to the commercial fishery calls first for an inquiry into the variability of ages and weights of blue pike sampled from different ports, sections of the lake, seasons of the year, and by different gears. This information is essential if data are to be combined or stratified to obtain the most dependable description of changes in the fishery.

The numbers of fish, age composition, types of gear, and average age, length, and weight of blue pike in fall samples from landings at different ports in 1943–59 are recorded in Table VI. Studies of the variability of mean ages, lengths, and weights are handicapped somewhat by year-to-year differences in port and gear. Continuous samples were not taken at any single port, and landings were sampled only from gill nets in 1945 and only from trap nets in 1951 and 1952.

To evaluate possible bias from port and gear of capture, the materials of Table VI were grouped by paired samples as listed in Table VII. The first line in the body of Table VII shows, for example, that a sample of blue pike taken by gill nets from a particular port averaged 0.3 year older and 0.1 oz lighter (16 comparisons) than samples taken farther west in the same year. (In this analysis a port not at the extreme eastern or western end of the lake can serve alternatively as "easterly" and "westerly.") Samples from trap nets yielded similar results; on the average (21 comparisons), fish from a particular port averaged 0.2 year older and 0.9 oz lighter than those in samples collected farther west.

Since data were lacking for a comparison of gill-net and trap-net samples collected in the same year at the same port, comparison was based on records from the closely adjacent gill-net grounds of Erie and trap-net grounds of Conneaut. Here the gill-net fish averaged 0.1 year older and 1.0 oz heavier than the trap-net fish (eight comparisons). The broader comparison (24 pairs) of gill-net and trap-net samples from all ports yielded the slightly greater difference of 0.2 year and 1.1 oz.

Table VII gives clear evidence that the mean age and weight of samples of blue pike from Lake Erie are influenced by port and gear of capture. Yet this bias is not great enough to be highly damaging when considered in relation to the actual average ages and weights of the different samples (Table VI). Consequently, all available collections for each year are employed, without separation according to port or gear, in later analyses of data on the strength and contribution of year-classes.

The collection of most of the samples in the fall raises the further question whether the data on year-class composition from fall samples are applicable the following spring. Since overwinter growth almost surely is inconsequential or nil and hence no significant recruitment of catchable-sized fish can take place, growth cannot change greatly the year-class composition and the size of blue pike in the fishery from the fall to the following spring. Questions exist, however, whether natural mortality, late fall and winter fishing mortality,[4] or seasonal differences in segregation by size and maturity of blue pike could impair the applicability of data from fall collections to analyses of data on the fishery of the following spring.

[4]In the years that scale samples were taken (1943–59), commercial fishing was open in all waters of Lake Erie except from December 21 to March 14 in Ohio, and January 1 to March 10 in Michigan. Even when fishing was legal, bad weather and ice greatly reduced fishing effort in late December through February.

TABLE VI. Percentages of total numbers of blue pike contributed by different age-groups in samples from commercial catches in the fall, and average ages, lengths, and weights of fish in the samples, Lake Erie, 1943–59. (The percentage of the total weight of the annual samples contributed by each age-group is given in parentheses. Asterisks indicate modes.)

Year and port	Gear[a]	No. of fish	Age-group[b]								Grand average		
			I	II	III	IV	V	VI	VII	VIII	Age[c]	Length (*inches*)	Weight (*ounces*)
1943													
Conneaut	T	208	–	0.5	43.7	55.3	0.5	–	–	–	3.6	11.8	8.3
Lorain	T	122	0.8	6.6	31.1	56.6	4.9	–	–	–	3.6	12.9	11.0
Erie	G	252	–	0.8	37.7	59.9	1.6	–	–	–	3.6	12.1	8.9
Vermillon	G	123	–	–	35.8	63.4	0.8	–	–	–	3.6	12.4	9.6
Total or average		705	0.1 (0.1)	1.6 (1.3)	38.0 (36.3)	58.6* (60.0)	1.7 (2.3)	– –	– –	– –	3.6 –	12.2 –	9.2 –
1944													
Conneaut	T	85	2.4	10.6	5.9	56.5	24.6	–	–	–	3.9	12.7	10.5
Erie	G	106	–	–	3.8	67.9	28.3	–	–	–	4.2	12.7	10.6
Lorain	G	73	–	24.6	15.1	48.0	12.3	–	–	–	3.4	13.2	12.0
Total or average		264	0.8 (0.4)	10.2 (9.5)	7.6 (7.3)	58.7* (59.1)	22.7 (23.7)	– –	– –	– –	3.9 –	12.8 –	11.0 –
1945													
Erie	G	221	–	3.2	4.5	54.3	31.2	6.8	–	–	4.3	13.4	11.2
Conneaut	G	179	0.6	37.4	11.7	29.6	19.6	1.1	–	–	3.3	12.3	8.4
Total or average		400	0.3 (0.2)	18.5 (12.6)	7.7 (6.9)	43.3* (45.0)	26.0 (30.2)	4.2 (5.1)	– –	– –	3.9 –	12.9 –	9.9 –
1946													
Conneaut	T	166	–	42.2	21.7	12.6	17.5	6.0	–	–	3.2	12.3	8.1
Sandusky	T	117	–	91.7	8.3	–	–	–	–	–	2.1	11.6	6.9
Lorain	G	55	–	21.8	25.4	31.0	20.0	1.8	–	–	3.5	14.1	13.4
Total or average		338	– –	56.0* (49.0)	17.7 (15.8)	11.3 (12.8)	11.8 (17.0)	3.2 (5.4)	– –	– –	2.7 –	12.3 –	8.5 –
1947													
Conneaut	T	342	–	7.6	88.3	2.9	0.6	0.6	–	–	3.0	11.7	7.6
Sandusky	T	199	–	4.0	91.0	5.0	–	–	–	–	3.0	12.5	8.7
Erie	G	150	–	23.3	59.4	11.3	6.0	–	–	–	3.0	11.6	7.0
Lorain	G	107	–	7.5	78.5	8.4	3.7	1.9	–	–	3.1	12.7	9.1
Total or average		798	– –	9.7 (9.7)	82.2* (77.6)	5.7 (8.2)	1.9 (3.4)	0.5 (1.1)	– –	– –	3.0 –	12.1 –	8.0 –

1948

Total or average			–	(9.7)	(77.6)	(8.2)	(3.4)	(1.1)					
1948													
Conneaut	T	197	–	–	2.5	97.0	0.5	–	–	–	4.0	11.7	8.0
Sandusky	T	250	–	–	6.4	90.8	1.6	0.8	0.4	–	4.0	12.8	10.5
Erie	G	233	–	–	2.6	94.4	3.0	–	–	–	4.0	11.9	8.4
Lorain	G	233	–	–	3.4	92.3	4.3	–	–	–	4.0	12.8	10.3
Total or average		913	–	–	3.8	93.5*	2.4	0.2	0.1	–	4.0	12.4	9.4
			–	–	(3.2)	(93.9)	(2.5)	(0.2)	(0.2)	–	–	–	–
1949													
Conneaut	T	180	–	–	1.1	11.1	86.1	1.7	–	–	4.9	12.2	8.6
Lorain	T	160	–	1.9	–	3.1	90.0	4.4	0.6	–	4.9	13.1	11.2
Erie	G	181	–	–	–	2.8	93.9	2.8	0.5	–	5.0	12.1	8.8
Total or average		521	–	0.6	0.4	5.7	90.0*	2.9	0.4	–	4.9	12.4	9.5
			–	(0.4)	(0.2)	(5.2)	(90.7)	(3.1)	(0.4)	–	–	–	–
1950													
Conneaut	T	136	1.5	1.5	3.0	27.9	44.8	21.3	–	–	4.8	12.3	8.3
Dunkirk	G	135	0.7	0.7	0.7	8.1	22.3	63.8	3.0	0.7	5.6	13.6	12.0
Erie	G	122	0.8	–	1.6	7.4	48.4	36.1	5.7	–	5.3	13.5	11.3
Total or average		393	1.0	0.8	1.8	14.7	38.2	40.4*	2.8	0.3	5.2	13.1	10.5
			(0.5)	(1.0)	(3.3)	(27.4)	(34.7)	(31.8)	(1.0)	(0.3)	–	–	–
1951													
Conneaut	T	214	–	8.9	9.8	21.5	34.5*	21.0	4.3	–	4.6	11.9	7.9
			–	(5.6)	(7.3)	(16.8)	(34.7)	(27.9)	(7.7)	–	–	–	–
1952													
Dunkirk	T	135	–	3.0	80.8	8.1	7.4	0.7	–	–	3.2	11.3	6.6
Erie	T	173	–	2.9	87.8	6.4	0.6	1.7	0.6	–	3.1	11.9	8.2
Conneaut	T	174	–	5.7	86.8	7.5	–	–	–	–	3.0	11.4	6.9
Sandusky	T	166	–	1.8	80.7	17.5	–	–	–	–	3.2	12.5	8.8
Total or average		648	–	3.4	84.2*	9.9	1.8	0.6	0.1	–	3.1	11.8	7.7
			–	(3.2)	(82.6)	(10.0)	(2.1)	(1.4)	(0.7)	–	–	–	–
1953													
Erie	T	125	–	3.2	17.6	72.8	3.2	1.6	–	1.6	3.9	12.3	8.2
Wheatley	P	173	–	1.7	21.5	67.4	5.9	2.9	0.6	–	3.9	11.5	7.9
Sandusky	T	144	'	2.1	4.9	90.2	2.8	–	–	–	4.0	12.8	10.3
Dunkirk	G	142	1.4	2.1	17.6	74.0	2.8	0.7	–	1.4	3.8	11.1	6.5
Lorain	G	124	–	0.8	9.7	86.3	3.2	–	–	–	3.9	12.5	8.8
Total or average		708	0.3	2.0	14.6	77.7*	3.8	0.9	0.1	0.6	3.9	12.2	8.3
			(0.1)	(1.6)	(13.3)	(76.9)	(4.0)	(1.7)	(0.2)	(2.2)	–	–	–

(*Continued*)

TABLE VI. Percentages of total numbers of blue pike contributed by different age-groups in samples from commercial catches in the fall, and average ages, lengths, and weights of fish in the samples, Lake Erie, 1943–59. (The percentage of the total weight of the annual samples contributed by each age-group is given in parentheses.) — (*Concluded*)

Year and port	Gear[a]	No. of fish	Age-group[b] I	II	III	IV	V	VI	VII	VIII	Grand average Age[c]	Length (*inches*)	Weight (*ounces*)
1954													
Lorain	T	127	0.2	64.8	12.7	6.4	15.9	–	–	–	2.7	12.8	10.4
Dunkirk	G	50	–	–	8.0	34.0	58.0	–	–	–	4.5	13.4	12.1
Erie	G	147	–	6.8	16.3	49.7	27.2	–	–	–	4.0	12.4	10.5
Wheatley	G	119	2.5	20.1	12.6	26.9	36.3	1.6	–	–	3.8	12.6	10.8
Total or		443	1.1	26.0	13.3	29.3	29.8*	0.5	–	–	3.6	12.7	10.7
average			(1.0)	(22.2)	(13.1)	(29.3)	(33.9)	(0.5)	–	–	–	–	–
1955													
Conneaut	T	155	12.3	7.7	21.9	27.7	20.0	9.7	0.6	–	3.7	14.3	17.3
Vermillon	T	104	18.3	15.4	39.4	7.7	6.7	12.5	–	–	3.1	14.9	19.5
Dunkirk	G	140	8.6	11.4	10.0	23.6	33.6	12.1	0.7	–	4.0	14.7	19.8
Erie	G	147	10.9	16.3	23.1	27.2	21.8	0.7	–	–	3.4	14.2	17.2
Wheatley	G	120	8.3	14.2	39.2	12.5	14.2	11.6	–	–	3.4	14.3	17.8
Total or		666	11.4	12.7	25.5*	20.9	20.1	9.1	0.3	–	3.5	14.4	18.2
average			(4.9)	(9.0)	(22.8)	(22.2)	(27.3)	(13.5)	(0.3)	–	–	–	–
1956													
Dunkirk	T	153	3.3	85.6	–	0.7	2.6	5.2	2.6	–	2.4	12.9	12.8
Erie	T	149	4.7	83.3	1.3	2.7	–	2.0	6.0	–	2.4	12.7	11.7
Conneaut	T	156	4.5	92.9	0.7	1.9	–	–	–	–	2.0	12.5	10.5
Sandusky	T	150	9.3	89.4	1.3	–	–	–	–	–	1.9	12.8	11.3
Erie	G	150	0.7	89.2	2.0	0.7	2.0	2.7	2.0	0.7	2.3	13.0	12.5
Vermilion	G	151	–	98.7	1.3	–	–	–	–	–	2.0	12.6	11.1
Wheatley	G	157	–	97.4	2.6	–	–	–	–	–	2.0	12.9	12.0
Total or		1066	3.2	91.0*	1.3	0.9	0.7	1.4	1.4	0.1	2.1	12.8	11.7
average			(2.4)	(85.1)	(1.4)	(2.2)	(1.6)	(3.1)	(3.9)	(0.3)	–	–	–
1957													
Erie	G	128	–	63.2	35.2	0,8	–	–	0.8	–	2.4	15.1	22.8
Dunkirk	T	112	3.6	58.8	25.0	2.7	1.8	4.5	0.9	2.7	2.7	14.8	19.2
Total or		240	1.7	61.2*	30.4	1.7	0.8	2.1	0.8	1.3	2.5	15.0	21.1
average			(0.9)	(52.6)	(32.7)	(2.9)	(2.0)	(5.1)	(1.5)	(2.3)	–	–	–
1958													
Several ports	T, G	109	–	3.7	42.2*	25.7	9.2	9.2	7.3	1.8	4.1	18.4	44.5
			–	(1.6)	(36.1)	(24.1)	(12.8)	(10.8)	(9.3)	(4.5)	–	–	–
1959													
Several ports	T, G	108	0.9	–	19.4	46.3*	10.2	9.3	9.3	3.7	4.5	19.8	60.5
			(0.4)	–	(14.9)	(37.8)	(11.6)	(11.1)	(15.2)	(7.0)	–	–	–

[a]T = trap net, G = gill net, P = pound net.
[b]No fish of age-group IX were collected; fish of age-group X were taken only in 1958 (0.9% of the number and 0.8% of the weight) and in 1959 (0.9% of the number and 2.0% of the weight).
[c]Average number of annuli on additional growing season had been practically completed at the time of collection.

TABLE VII. Differences in average age (numbers of completed annuli) and weight (ounces) as determined from various groupings of paired samples. (Both samples of each pair were collected in the same year; table is based on data of Table VI.)

Basis of comparison	Number of paired samples	Mean difference between averages[a]	
		Age	Weight (*ounces*)
Easterly and westerly[b] ports (gill nets)	16	0.3	−0.1
Easterly and westerly ports (trap nets)	21	0.2	−0.9
Gill nets (Erie) and trap nets (Conneaut)	8	0.1	1.0
Gill nets (all ports) and trap nets (all ports)	24	0.2	1.1

[a]Unweighted mean of differences for individual pairings; in each individual comparison the average age or weight of the sample falling in the second group was subtracted from that of the sample falling in the first group.

[b]As an example, in 1943 (Table VI) the port of Erie is "easterly" and Vermillon is "westerly" (gill nets), and the port of Conneaut is "easterly" and Lorain "westerly" for trap nets.

A detailed comparison of year-class composition in fall and the following spring is not possible because only two spring collections are available. The relation between the year-class composition of the collections in the spring and the preceding fall was not the same in the two pairs of samples (Table VIII).

The agreement between the spring collection at Wheatley in 1952 and the collection of the preceding fall at Conneaut (no sample from Wheatley in the fall of 1951) was reasonably good. The dominant 1945 year-class contributed 34.5% of the total in both seasons and the difference of only 0.3 year in mean age (5.6 growing seasons in the fall and 5.3 in the spring) was inconsequential. On the other hand, the year-class compositions of blue pike collected at Conneaut in April 1951 and in October 1950 did not agree equally well. The fall collection was dominated by the 1945 year-class (44.8% but dominance shifted to the 1946 year-class (36.0%) in the April 1951 sample. The difference in mean age (5.8 growing seasons in the fall, 5.1 in the spring) was more than twice the difference between the mean ages of fish collected in the fall of 1951 and in the spring of 1952.

The evidence from the two comparisons throws doubt on the usefulness of data on year-class composition of fall samples for the analysis of statistics for the spring fishery. Despite the probability that factors or events that affected the fall fishery also affected the spring fishery, sampling errors in the fall would be greatly magnified if applied to the high production period in the spring; consequently, the description of the year-class contributions that follows is restricted to the fall fishery.

AGE AND YEAR-CLASS COMPOSITION

The age composition of blue pike in the 1943–59 samples varied widely from year to year (Table VI, Fig. 4). Samples were dominated by age-group

TABLE VIII. Year-class compositions (expressed as percentages) of blue pike taken in the spring and fall, 1950–52.

Seasons compared and ports of capture	Date of collection	No. of fish	Year-class											Average age[a]
			1940	1941	1942	1943	1944	1945	1946	1947	1948	1949		
Fall 1951; spring 1952														
Conneaut	October 4, 1951	214	–	–	–	4.3	21.0	34.5	21.5	9.8	8.9	–		5.6
Wheatley	April 2, 1952	122	–	–	–	1.6	17.2	34.5	18.8	10.7	17.2	–		5.3
Fall 1950; spring 1951														
Conneaut	October 19, 1950	136	–	–	–	–	21.3	44.8	27.9	3.0	1.5	1.5		5.8
Conneaut	April 23, 1951	353	0.3	–	0.3	0.8	7.1	26.6	36.0	24.4	3.4	1.1		5.1

[a]Number of growing seasons.

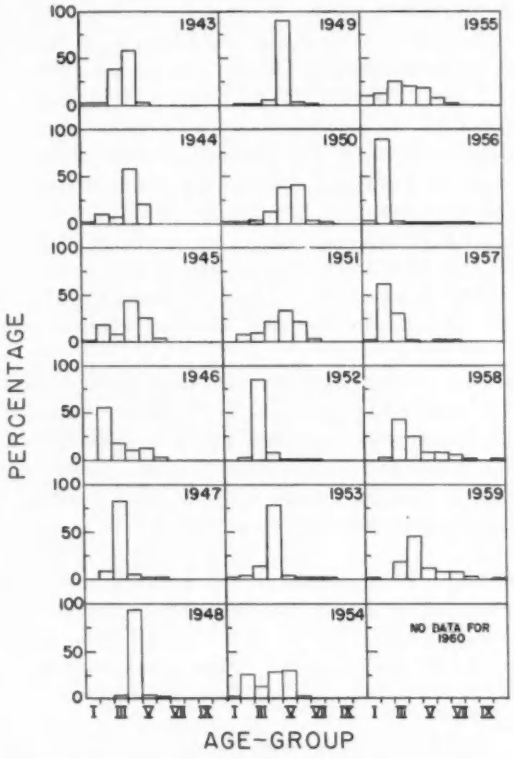

FIG. 4. Age compositions (expressed in percentages of total numbers) of samples of blue pike, 1943–59.

IV in 6 of the 17 years, by age-group III in 4 years, II in 3, V in 3, and VI in 1 year. Dominance or unusual strength of age-groups usually was attributable to the strength of particular year-classes.

The successive dominance of age-groups II though VI in 1946–50 demonstrates the overwhelming effect of the 1944 year-class on the age composition of the blue pike over this period (Table VI). The 1949 year-class had a similar, though less pronounced, effect on age composition in 1952–54. The only other year-class that dominated the fishery more than 1 year was the weak 1955 year-class, which appeared during the collapse of the fishery.

Age-groups VII and older appeared to be relatively stronger in the catches after 1954, probably due to declining numbers of younger fish and increased fishing with large-mesh gill nets rather than to an increase in actual abundance of older fish.

Lengths and Weights

Length distributions and modes of the samples of blue pike (Table IX) exhibit clearly an increase of modal lengths within each of the periods 1943–45, 1946–50, 1951–55, and 1956–59. These periods of increase appear to have been closely related to the increases in length of dominant year-classes as they passed through the fishery. For example, during 1946–50, when the 1944 year-class dominated the samples, average lengths of this year-class increased progressively from 11.5 inches to 13.4 inches (Table X), and the mode of all fish in the samples increased from 11.0–11.4 to 13.5–13.9 inches (Table IX). The strong 1939 and 1940 year-classes were largely responsible for the increases in modal lengths from 1943 to 1945, as were the 1949 year-class from 1952 to 1954 and the fast growing 1954 and 1955 year-classes from 1956 to 1959.

Despite the effect of dominant year-classes on short-term trends in length distribution, mean lengths of blue pike in the fishery varied little from 1943 to 1954 (Table X). The average lengths of fish in samples fell within the limited range of 11.8–13.1 inches and fluctuations of average lengths of the different age-groups showed no distinct trends. For example, average lengths of fish of age-group III fluctuated only between 11.0 and 12.7 inches during the 12 years.

The average length of blue pike in the samples, and in each age-group and year-class, increased substantially after 1954 except in 1956. The average length changed from 14.4 in 1955 to 19.8 in 1959. The decrease from 14.4 inches in 1955 to 12.8 in 1956 was due to the strong representation of young fish (age-group II) in the fishery (average age dropped from 3.5 years in 1955 to 2.1 in 1956).

The increase in average length of fish of an age-group in successive years is best demonstrated by age-group IV: average lengths from 1954 to 1959 were 12.5, 14.8, 16.4, 17.7, 18.4, and 18.9 inches. Other well-represented age-groups (except II and III in 1956) showed similar increases in length.

Since the 1954 and 1955 year-classes contributed 78% of the catches from 1956 to 1959, these two year-classes describe generally the increase in both length and growth rate of blue pike after 1954. Average lengths of the 1954 year-class as age-groups I to V, from 1955 to 1959, were 11.6, 12.6, 15.3, 18.4, and 20.4 inches (annual increments 1.0, 2.7, 3.1, and 2.0 inches). Average lengths of the 1955 year-class as age-groups I to IV, from 1956 to 1959, were 11.8, 14.5, 17.8, and 18.9 inches (annual increments, 2.7, 3.3, and 1.1 inches).

The average weights of blue pike of each age-group in the annual collections also show the increase in growth rate and size after 1954 (Table XI). In 1943–54 the average weights of fish (age-groups combined) in the collections ranged from 7.7 oz to 11.0 oz, but in 1955–59 the range of the means was 11.7 to 60.5 oz. The average weight was lowest in 1952 and highest in 1959. Average weights of the individual age-groups (I to VIII) ranged from 5.0 to 13.1 oz in 1950 and from 23.0 to 114.3 oz in 1959. Blue pike of age-group III were almost eight times heavier in 1959 than in 1951.

TABLE IX. Percentage length distributions of blue pike in samples from the commercial fishery of Lake Erie, 1943–59. (Asterisks indicate modes.)

TABLE IX. *Percentage length distributions of blue pike in samples from the commercial fishery of Lake Erie, 1943–59. (Asterisks indicate modes.)*

Length (*inches*)	Year of collection																
	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
7.5– 7.9	–	–	–	–	–	–	–	–	–	–	0.3	–	–	–	–	–	–
8.5– 8.9	–	–	–	–	–	–	–	–	–	0.1	–	–	–	–	–	–	–
9.0– 9.4	–	–	–	–	–	–	–	0.2	0.9	–	0.5	–	–	–	–	–	–
9.5– 9.9	–	–	1.4	–	0.6	–	–	0.5	0.9	0.1	2.8	–	–	0.1	–	–	–
10.0–10.4	0.6	0.6	1.4	1.2	4.8	2.0	1.7	0.2	5.6	4.1	4.6	–	–	0.2	–	–	–
10.5–10.9	2.9	1.8	5.8	6.1	14.5	9.1	4.4	2.0	8.9	13.4	6.8	0.5	0.8	2.3	–	–	–
11.0–11.4	10.3	2.2	5.8	20.1*	18.0*	20.3	15.0	4.5	20.5*	20.7	11.0	3.6	3.9	4.4	–	–	–
11.5–11.9	17.7	8.6	7.6	16.7	14.4	32.6*	22.1	6.7	17.7	23.7*	16.1	11.4	8.0	14.3	0.5	–	–
12.0–12.4	25.0*	18.6	6.9	10.2	12.3	22.9	25.0*	12.2	11.7	16.1	18.5*	15.6	3.2	20.7	1.8	–	–
12.5–12.9	21.3	25.9*	14.2	4.7	11.9	8.6	17.8	13.0	11.7	12.1	12.5	15.6	5.1	22.7*	2.2	–	–
13.0–13.5	11.4	22.0	20.2*	8.5	9.9	2.5	7.8	18.4	7.5	5.6	13.4	28.6*	6.2	18.8	6.4	–	–
13.5–13.9	5.1	11.9	17.5	8.2	6.5	1.0	3.9	19.6*	5.1	2.8	5.7	14.7	7.9	7.4	11.9	–	–
14.0–14.4	4.8	7.2	11.1	6.0	4.0	1.0	1.7	13.6	2.3	0.9	3.8	6.7	10.9	3.1	21.9*	–	–
14.5–14.9	0.4	1.2	5.6	4.0	2.2	–	0.6	6.6	1.9	0.1	1.7	1.7	11.4*	0.7	14.4	1.8	–
15.0–15.4	0.3	–	2.2	8.1	0.9	–	–	2.1	1.4	–	1.2	0.3	9.3	1.0	13.0	1.8	1.2
15.5–15.0	0.2	–	0.3	3.0	–	–	–	0.2	0.5	–	0.2	0.3	7.1	0.9	8.5	2.8	–
16.0–16.4	–	–	–	1.6	–	–	–	–	0.5	0.2	0.2	1.0	8.1	1.1	6.6	0.9	1.2
16.5–16.9	–	–	–	1.4	–	–	–	0.2	0.5	–	0.2	–	4.8	1.1	2.2	8.3	–
17.0–17.4	–	–	–	0.2	–	–	–	–	0.5	–	–	–	5.2	0.1	3.2	9.1	5.0
17.5–17.9	–	–	–	–	–	–	–	–	0.9	0.1	0.2	–	4.0	0.4	2.5	11.9	5.0
18.0–18.4	–	–	–	–	–	–	–	–	–	–	–	–	1.7	0.4	2.6	19.3*	7.5
18.5–18.9	–	–	–	–	–	–	–	–	0.5	–	0.3	–	0.6	–	–	16.5	15.0*
19.0–19.4	–	–	–	–	–	–	–	–	–	–	–	–	0.8	0.3	1.4	7.3	13.8
19.5–19.9	–	–	–	–	–	–	–	–	0.5	–	–	–	0.3	–	0.9	5.5	3.8
20.0–20.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.8	8.8
20.5–20.9	–	–	–	–	–	–	–	–	–	–	–	–	0.7	–	–	3.7	7.5
21.0–21.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.8	5.0
21.5–21.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.9	3.8
22.0–22.4	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	–	2.8	5.0
22.5–22.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.9	1.2
23.0–23.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.4
23.5–23.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.8
24.0–24.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.8
24.5–24.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.8
25.0–25.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.4
26.0–26.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.9	–
No. of fish	705	264	400	338	798	913	521	393	214	648	708	443	666	1066	240	109	108
Mean length	12.2	12.8	12.9	12.3	12.1	12.4	12.4	13.1	11.9	11.8	12.2	12.7	14.4	12.8	15.0	18.5	19.8

TABLE X. Average total lengths (inches) of blue pike for different age-groups and years of collection, Lake Erie, 1943–59. (Numbers of fish in parentheses.)

Year	Age-group[a] I	II	III	IV	V	VI	VII	VIII	X	Average
1943	11.2	11.8	11.9	12.3	13.8	–	–	–	–	12.2
	(1)	(11)	(268)	(413)	(12)	–	–	–	–	(705)
1944	10.9	12.2	12.6	12.9	13.1	–	–	–	–	12.8
	(2)	(27)	(20)	(155)	(60)	–	–	–	–	(264)
1945	11.5	11.2	12.2	13.3	13.6	13.9	–	–	–	12.9
	(1)	(74)	(31)	(173)	(104)	(17)	–	–	–	(400)
1946	–	11.5	12.3	13.8	14.4	14.8	–	–	–	12.3
	–	(191)	(58)	(38)	(40)	(11)	–	–	–	(338)
1947	–	11.0	12.0	13.6	14.4	16.0	–	–	–	12.1
	–	(77)	(656)	(46)	(15)	(4)	–	–	–	(798)
1948	–	–	11.6	12.4	12.5	13.0	–	16.6	–	12.4
	–	–	(35)	(853)	(22)	(2)	–	(1)	–	(913)
1949	–	11.9	11.1	11.9	12.4	13.0	12.2	–	–	12.4
	–	(3)	(2)	(30)	(469)	(15)	(2)	–	–	(521)
1950	10.2	11.4	12.2	12.7	13.1	13.4	13.7	14.2	–	13.1
	(4)	(3)	(7)	(58)	(150)	(159)	(11)	(1)	–	(393)
1951	–	10.6	11.0	11.2	12.0	13.0	14.5	–	–	11.9
	–	(19)	(21)	(46)	(74)	(45)	(9)	–	–	(214)
1952	–	11.3	11.8	11.9	12.6	13.9	17.1	–	–	11.8
	–	(22)	(546)	(64)	(11)	(4)	(1)	–	–	(648)
1953	9.9	11.1	11.9	12.2	12.4	12.8	12.7	17.8	–	12.2
	(2)	(14)	(103)	(549)	(26)	(9)	(1)	(4)		(708)
1954	12.3	12.4	12.7	12.5	13.2	13.4	–	–	–	12.7
	(5)	(115)	(59)	(130)	(132)	(2)	–	–	–	(443)
1955	11.6	13.3	14.1	14.8	15.9	16.5	15.6	–	–	14.4
	(76)	(85)	(170	(139))	(134)	(60)	(2)	–	–	(666)
1956	11.8	12.6	13.0	16.4	16.8	16.7	16.8	17.8	–	12.8
	(34)	(970)	(14)	(6)	(10)	(15)	(16)	(1)	–	(1,066)
1957	12.4	14.5	15.3	17.7	18.0	18.7	17.7	18.2	–	15.0
	(4)	(147)	(73)	(4)	(2)	(5)	(2)	(3)	–	(240)
1958	–	15.0	17.8	18.4	20.0	19.2	19.9	24.0	18.4	18.5
	–	(4)	(46)	(28)	(10)	(10)	(8)	(2)	(1)	(109)
1959	15.0	–	18.7	18.9	20.4	20.6	23.1	23.7	24.7	19.8
	(1)	–	(21)	(50)	(11)	(10)	(10)	(4)	(1)	(108)

[a]Fish in these fall collections had completed or nearly completed the growing season in the year of capture (e.g. fish in age-group I had completed two growing seasons). Age-group IX was not represented in the collections.

The average weights of blue pike of the strong year-classes of 1944, 1949, and 1954 in successive annual samples further demonstrate the increased growth rate of fish of all ages after 1954 (Fig. 5). The 1944 year-class grew slowly; average weights were 6.5 oz as age-group I (1 fish) and 14.4 oz at age-group VII; annual increments were 0.1 to 3.1 oz. The average weight of fish of the

TABLE XI. Average weights (ounces) of blue pike in different age-groups and years of collection, Lake Erie, 1943–59. (Numbers of fish in parentheses.)

Year	Age-group[a] I	II	III	IV	V	VI	VII	VIII	X	Average
1943	7.0	8.2	8.6	9.5	13.8	–	–	–	–	9.2
	(1)	(11)	(268)	(413)	(12)	–	–	–	–	(705)
1944	5.4	9.2	10.7	11.1	11.5	–	–	–	–	11.0
	(2)	(27)	(20)	(155)	(60)	–	–	–	–	(264)
1945	6.5	6.0	8.2	10.6	11.7	12.8	–	–	–	9.9
	(1)	(74)	(31)	(173)	(104)	(17)	–	–	–	(400)
1946	–	6.6	8.2	11.8	13.6	14.3	–	–	–	8.5
	–	(191)	(58)	(38)	(40)	(11)	–	–	–	(338)
1947	–	5.9	7.8	11.3	14.1	15.5	–	–	–	8.0
	–	(77)	(656)	(46)	(15)	(4)	–	–	–	(798)
1948	–	–	7.9	9.4	9.8	10.1	–	22.8	–	9.4
	–	–	(35)	(853)	(22)	(2)	–	(1)	–	(913)
1949	–	7.8	6.0	8.0	9.5	10.6	9.1	–	–	9.5
	–	(3)	(2)	(30)	(469)	(15)	(2)	–	–	(521)
1950	5.0	6.3	8.2	9.2	10.3	11.3	12.2	13.1	–	10.5
	(4)	(3)	(7)	(58)	(150)	(159)	(11)	(1)	–	(393)
1951	–	5.0	5.9	6.2	7.9	10.4	14.4	–	–	7.9
	–	(19)	(21)	(46)	(74)	(45)	(9)	–	–	(214)
1952	–	7.0	7.5	8.0	8.5	18.1	32.0	–	–	7.7
	–	(22)	(546)	(64)	(11)	(4)	(1)	–	–	(648)
1953	1.8	6.7	7.3	8.4	9.0	11.5	11.4	28.8	–	8.3
	(2)	(14)	(103)	(549)	(26)	(9)	(1)	(4)	–	(708)
1954	9.4	9.2	10.5	10,7	12.2	12.3	–	–	–	10.7
	(5)	(115)	(59)	(130)	(132)	(2)	–	–	–	(443)
1955	7.8	12.7	16.2	19.1	24.8	27.9	22.2	–	–	18.2
	(76)	(85)	(170)	(139)	(134)	(60)	(2)	–	–	(666)
1956	8.5	10.9	12.2	26.3	32.7	27.7	31.8	36.0	–	11.7
	(34)	(970)	(14)	(6)	(10)	(15)	(16)	(1)	–	(1,066)
1957	10.8	18.4	23.2	34.5	43.8	46.7	39.8	35.7	–	21.1
	(4)	(147)	(73)	(4)	(2)	(5)	(2)	(3)		(240)
1958	–	19.5	38.1	41.9	62.1	52.6	56.1	103.0	40.0	44.5
	–	(4)	(46)	(28)	(10)	(10)	(8)	(2)	(1)	(109)
1959	23.0	–	46.5	49.4	68.8	72.5	99.2	114.3	128.8	60.5
	(1)	–	(21)	(50)	(11)	(10)	(10)	(4)	(1)	(108)

[a]Fish in these fall collections had completed or nearly completed the growing season in the year of capture (e.g. fish in age-group I had completed two growing seasons). Age-group IX was not represented in the collections.

1949 year-class was 5.0 oz as age-group I and 12.2 oz as age-group V, but then increased to 31.8 oz as age-group VII in 1956. Weight of fish of the 1954 year-class increased from 7.8 oz in 1955 (age-group I) to 68.8 oz in 1959 (age-group V); successive annual increments in ounces were 3.1, 12.3, 18.7, and 26.9.

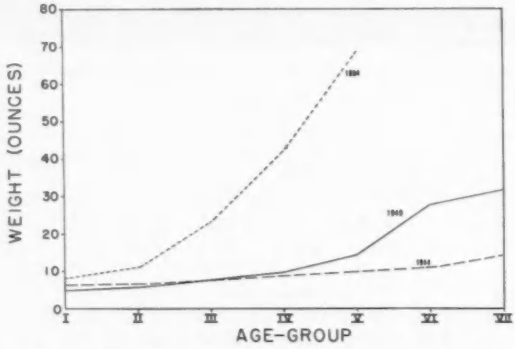

FIG. 5. Average weights (ounces) of blue pike of the year-classes 1944 (long dashes), 1949 (solid line), and 1954 (short dashes) at different ages.

Average weights of age-groups III, IV, and V in successive annual samples also demonstrate the changes in the size of fish in the fishery (Fig. 6). The greatest increases in weight, which occurred after 1956, were coincident with the sharp decline in commercial production.

CONTRIBUTIONS OF YEAR-CLASSES

Contributions of year-classes to the fall production of blue pike were estimated for year-classes that contributed all or most of their production

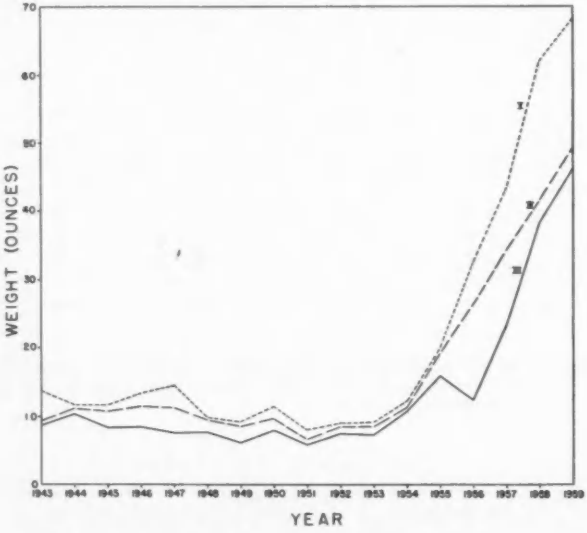

FIG. 6. Average weights of age-group III (solid line), age-group IV (long dashes), and age-group V (short dashes) of blue pike samples from the fall commercial landings of Lake Erie, 1943–59.

from 1941 to 1959. Of the 20 year-classes represented in the 1943–59 samples, contributions were estimated for the 18 consecutive year-classes 1939–56. Omitted from the estimated contributions were the 1938 year-class, which appeared only in the 1943 samples, and the 1958 year-class, which constituted less than 1% of the 1959 sample.

Contributions of year-classes were estimated by both number and weight. The percentages by number and weight of each age-group in the annual samples (from Table VI) were applied directly to the total fall catch for the year of each sample.

Since production was not recorded by season for the entire lake, estimates of fall production each year in Pennsylvania, New York, and Ontario and for some years in Ohio were based on the percentage production in the fall fishery (September–December) in Ohio in 1948–59 (Table XII). The average

TABLE XII. Spring and fall production (thousands of pounds) of blue pike in Ohio waters and estimated spring and fall production for all waters in Lake Erie, 1948–59. (Percentages given in parentheses.)

	Production in Ohio waters			Production in all waters (estimated)		
Year	Spring[a]	Fall	Total	Spring	Fall	Total
1948	3,131 (45)	3,826 (55)	6,957	6,635	8,110	14,745
1949	7,962 (75)	2,654 (25)	10,616	17,837	5,946	23,783
1950	4,116 (84)	784 (16)	4,900	12,433	2,368	14,801
1951	1,419 (76)	448 (24)	1,867	4,609	1,455	6,064
1952	885 (16)	4,646 (84)	5,531	2,249	11,789	14,038
1953	4,934 (72)	1,919 (28)	6,853	13,320	5,145	18,375
1954	2,974 (65)	1,602 (35)	4,576	9,358	5,038	14,396
1955	2,869 (78)	810 (22)	3,679	15,354	4,331	19,685
1956	2,916 (62)	1,787 (38)	4,703	11,691	7,166	18,857
1957	2,653 (91)	262 (9)	2,915	9,437	933	10,370
1958	362 (99)	4 (1)	366	1,245	154	1,339
1959	19 (94)	1 (6)	20	75	4	79

[a]For purposes of licensing and reporting, the "spring" fishing season in Ohio is from March 15 to August 31 and the "fall" season is from September 1 to December 20.

percentage of the annual production landed in the fall in Ohio from 1948 to 1956 (36%) was used to estimate fall production in all years in Ontario, New York, and Pennsylvania, and in Ohio in 1941–47.

The weight contributions of age-groups II and III of the 1939 year-class in 1941 and 1942 and age-group II of the 1940 year-class in 1942 were estimated to complete the record of the total contributions of these year-classes to the fishery. The estimates were based on long-term (1943–54) ratios of catches among age-groups II to VI. These ratios were computed by dividing the estimated production of each of age-groups II to VI separately into the estimated production of each younger age-group. Ratios of production for each age-group were: age-group II was 0.18 of age-group III, 0.09 of age-group IV, 0.07 of age-group V, and 0.13 of age-group VI; and age-group III was 0.46 of age-group IV, 0.39 of age-group V, and 0.70 of age-group VI. As an example, the estimate of the pounds of fish produced in 1941 by age-group II of the 1939 year-class was determined by multiplying its estimated production in 1942 (as age-group III) by 0.18, in 1943 (as age-group IV) by 0.09, in 1944 (as age-group V) by 0.07, and in 1945 (as age-group VI) by 0.13, and then averaging the products.

The numbers of fish of the 1939 and 1940 year-classes produced in 1941–42 were estimated by dividing the number of fish per pound (based on the average weights of fish in each of the age-groups II and III in the samples collected in 1943–54) into the estimated poundage for each age-group.

The estimated contributions of only 5 of the 18 year-classes (1939, 1940, 1944, 1949, 1954) in the fishery exceeded the 1941–59 mean (Table XIII). The 1944 and 1949 year-classes dominated the catch and the two combined contributed 46.4% by number and 41.6% by weight (Table XIV) of the total 1941–59 fall catch from the 1939–56 year-classes. Fish of one or both of the 1944 and 1949 year-classes were present in the fishery from 1945 to 1959. The extent to which the 1944 and 1949 year-classes dominated the fall fishery during these years is demonstrated graphically in Fig. 7. The 1944 year-class contributed 28,155,000 fish (21.9% of the 1941–59 total and 394.7% of the 1941–59 mean contribution of year-classes 1939–56) or 16,083,000 lb (371.0% of the mean for all year-classes). The 1949 year-class contributed 31,407,000 fish (24.5% of the total and 440.3% of the mean of year-classes) or 16,385,000 lb (378.2% of the mean of year-classes).

Less important contributions were made by year-classes 1939 (11,995,000 fish, 9.3% of the total), 1940 (14,641,000 fish, 11.4%), and 1954 (9,597,000 fish, 7.5%); their combined contribution to the total was 28.2%. The other 13 year-classes together contributed only 25.3% of the fish produced by the 1939–56 year-classes. No fish of the 1957 year-class and only one fish of the 1958 year-class were collected, even though fish of both year-classes should have been well above commercial length by the fall of 1959.

Slightly greater percentage contributions by weight than by numbers were made by the 1950–56 year-classes, which were in the fishery after 1954,

Year-class	Year of capture																			Total for year-class		
	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	No. of fish	Percentage of 1941–59 total	Percentage of 1941–59 mean
1939																						
Age	II	III	IV	V	VI	–	–		–	–	–	–	–	–	–	–	–	–	–			
Number	287	1,522	6,955	2,882	349	–	–	–	–	–	–	–	–	–	–	–		–	–	11,995	9.3	168.2
Percentage	10.1	23.4	58.6	22.7	4.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–			
1940																						
Age	–	II	III	IV	V	VI	–	–	–	–	–	–	–	–	–	–	–	–	–			
Number	–	412	4,510	7,452	2,160	107	–	–	–	–	–	–	–	–	–	–	–	–	–	14,641	11.4	205.3
Percentage	–	6.3	38.0	58.7	26.0	3.2	–	–	–	–	–	–	–	–	–	–	–	–	–			
1941																						
Age	–	–	II	III	IV	V	VI	VII	–	–	–	–	–	–	–	–	–	–	–			
Number	–	–	190	965	3,596	393	17	14	–	–	–	–	–	–	–	–	–	–	–	5,175	4.0	72.5
Percentage	–	–	1.6	7.6	43.3	11.8	0.5	0.1	–	–	–	–	–	–	–	–	–	–	–			
1942																						
Age	–	–	I	II	III	IV	V	VI	VII	VIII	–	–	–	–	–	–	–	–	–			
Number	–	–	12	1,295	641	376	65	28	40	11	–	–	–	–	–	–	–	–	–	2,468	1.9	34.6
Percentage	–	–	0.1	10.2	7.7	11.3	1.9	0.2	0.4	0.3	–	–	–	–	–	–	–	–	–			
1943																						
Age	–	–	–	I	II	III	IV	V	VI	VII	–	–	–	–	–	–	–	–	–			
Number	–	–	–	102	1,538	590	196	330	290	101	–	–	–	–	–	–	–	–	–	3,147	2.5	44.1
Percentage	–	–	–	0.8	18.5	17.7	5.7	2.4	2.9	2.8	–	–	–	–	–	–	–	–	–			
1944																						
Age	–	–	–	–	I	II	III	IV	V	VI	VII	–	–	–	–	–	–	–	–			
Number	–	–	–	–	25	1,865	2,821	12,873	8,990	1,453	128	–	–	–	–	–	–	–	–	28,155	21.9	394.7
Percentage	–	–	–	–	0.3	56.0	82.2	93.5	90.0	40.4	4.3	–	–	–	–	–	–	–	–			
1945																						
Age	–	–	–	–	–	–	II	III	IV	V	VI	VII	VIII	–	–	–	–	–	–			
Number	–	–	–	–	–	–	333	523	569	1,375	627	24	60	–	–	–	–	–	–	3,511	2.7	49.2
Percentage	–	–	–	–	–	–	9.7	3.8	5.7	38.2	21.0	0.1	0.6	–	–	–	–	–	–			
1946																						
Age	–	–	–	–	–	–	–	–	III	IV	V	VI	VII	–	–	–	–	–	–			
Number	–	–	–	–	–	–	–	–	40	529	1,030	147	10	–	–	–	–	–	–	1,756	1.4	24.6
Percentage	–	–	–	–	–	–	–	–	0.4	14.7	34.5	0.6	0.1	–	–	–	–	–	–			
1947																						
Age	–	–	–	–	–	–	–	–	II	III	IV	V	VI	–	–	–	–	–	–			
Number	–	–	–	–	–	–	–	–	60	65	641	441	89	–	–	–	–	–	–	1,296	1.0	18.2
Percentage	–	–	–	–	–	–	–	–	0.6	1.8	21.5	1.8	0.9	–	–	–	–	–	–			
1948																						
Age	–	–	–	–	–	–	–	–	–	II	III	IV	V	VI	VII	VIII	–	X	–			
Number	–	–	–	–	–	–	–	–	–	29	292	2,428	377	38	11	10	–	–	–	3,185	2.5	44.6
Percentage	–	–	–	–	–	–	–	–	–	0.8	9.8	9.9	3.8	0.5	0.3	0.1	–	0.9	–			

(*Continued*)

TABLE XIII. Numbers (thousands) of fish and percentages of the total numbers contributed by different year-classes of blue pike to the fall fishery of Lake Erie, 1941–59.[a] (*Concluded*)

	Year of capture																			Total for year-class		
Year-class	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	No. of fish	Percentage of 1941–59 Total	Percentage of 1941–59 mean
1949																						
Age	–	–	–	–	–	–	–	–	–	I	II	III	IV	V	VI	VII	VIII	–	X			
Number	–	–	–	–	–	–	–	–	–	36	265	20,647	7,714	2,252	347	137	9	–	–	31,407	24.5	440.3
Percentage	–	–	–	–	–	–	–	–	–	1.0	8.9	84.2	77.7	29.8	9.1	1.4	1.3	–	0.9			
1950																						
Age	–	–	–	–	–	–	–	–	–	–	–	II	III	IV	V	VI	VII	VIII	–			
Number	–	–	–	–	–	–	–	–	–	–	–	834	1,450	2,214	766	137	6	1	–	5,408	4.2	75.8
Percentage	–	–	–	–	–	–	–	–	–	–	–	3.4	14.6	29.3	20.1	1.4	0.8	1.8	–			
1951																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	II	III	IV	V	VI	VII	VIII			
Number	–	–	–	–	–	–	–	–	–	–	–	–	200	1,005	797	69	15	4	–	2,090	1.6	29.3
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	2.0	13.3	20.9	0.7	2.1	7.3	3.7			
1952																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	I	II	III	IV	V	VI	VII			
Number	–	–	–	–	–	–	–	–	–	–	–	–	30	1,965	972	88	6	5	–	3,066	2.4	43.0
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	0.3	26.0	25.5	0.9	0.8	9.2	9.3			
1953																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	–	I	II	III	IV	V	VI			
Number	–	–	–	–	–	–	–	–	–	–	–	–	–	83	484	128	12	5	–	712	0.6	10.0
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	–	1.1	12.7	1.3	1.7	9.2	9.3			
1954																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	–	–	I	II	III	IV	V			
Number	–	–	–	–	–	–	–	–	–	–	–	–	–	–	434	8,934	215	14	–	9,597	7.5	134.5
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11.4	91.0	30.4	25.7	10.2			
1955																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	I	II	III	IV			
Number	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	314	434	24	1	773	0.6	10.8
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.2	61.2	42.2	46.3			
1956																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	I	II	III			
Number	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12	2	–	14	–	–
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.7	3.7	19.4			
Total	287	1,934	11,667	12,696	8,309	3,331	3,432	13,768	9,989	3,599	2,983	24,521	9,930	7,557	3,811	9,817	709	55	1	128,396		

[a]Year-class contributions of less than 500 fish and percentages less than 0.05 are not recorded.

[b]Since contributions of only the 1939 and 1940 year-classes were estimated for 1941 and 1942, and the 1938 year-class contribution was omitted in 1943, the only year it appeared in the samples, estimated contributions in 1941 to 1943 are less than the local production in those years and percentages do not equal 100; age-group I (1 fish, 0.9 %) in 1959 omitted.

[a]Year-class contributions of less than 500 fish and percentages less than 0.05 are not recorded.

[b]Since contributions of only the 1939 and 1940 year-classes were estimated for 1941 and 1942, and the 1938 year-class contribution was omitted in 1943, the only year in which appeared in the samples, estimated contributions in 1941 to 1943 are less than the local production in those years and percentages do not equal 100; age-group I (1 fish, 0.9 %) in 1959 omitted.

	Year of capture																				Total for year-class		
Year-class	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	Pounds	Percentage of 1941–59 total	Percentage of 1941–59 mean
1939																							
Age	II	III	IV	V	VI	–	–	–	–	–	–	–	–	–	–	–	–	–	–				
Pounds	183	973	4,189	2,075	263	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7,679	9.8	177.2	
Percentage	10.5	25.4	60.0	23.7	5.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–				
1940																							
Age	–	II	III	IV	V	VI	–	–	–	–	–	–	–	–	–	–	–	–	–				
Pounds	–	261	2,534	5,175	1,558	96	–	–	–	–	–	–	–	–	–	–	–	–	–	9,624	12.3	222.1	
Percentage	–	6.8	36.3	59.1	30.2	5.4	–	–	–	–	–	–	–	–	–	–	–	–	–				
1941																							
Age	–	–	II	III	IV	V	VI	VII	–	–	–	–	–	–	–	–	–	–	–				
Pounds	–	–	91	639	2,322	301	19	16	–	–	–	–	–	–	–	–	–	–	–	3,388	4.3	78.2	
Percentage	–	–	1.3	7.3	45.0	17.0	1.1	0.2	–	–	–	–	–	–	–	–	–	–	–				
1942																							
Age	–	–	I	II	III	IV	V	VI	VII	VIII	–	–	–	–	–	–	–	–	–				
Pounds	–	–	7	832	356	227	58	16	24	7	–	–	–	–	–	–	–	–	–	1,527	2.0	35.2	
Percentage	–	–	0.1	9.5	6.9	12.8	3.4	0.2	0.4	0.3	–	–	–	–	–	–	–	–	–				
1943																							
Age	–	–	–	I	II	III	IV	V	VI	VII	–	–	–	–	–	–	–	–	–				
Pounds	–	–	–	35	650	280	141	203	184	24	–	–	–	–	–	–	–	–	–	1,517	1.9	35.0	
Percentage	–	–	–	0.4	12.6	15.8	8.2	2.5	3.1	1.0	–	–	–	–	–	–	–	–	–				
1944																							
Age	–	–	–	–	I	II	III	IV	V	VI	VII	–	–	–	–	–	–	–	–				
Pounds	–	–	–	–	10	868	1,332	7,615	5,393	753	112	–	–	–	–	–	–	–	–	16,083	20.6	371.0	
Percentage	–	–	–	–	0.2	49.0	77.6	93.9	90.7	31.8	7.7	–	–	–	–	–	–	–	–				
1945																							
Age	–	–	–	–	–	–	II	III	IV	V	VI	VII	VIII	–	–	–	–	–	–				
Pounds	–	–	–	–	–	–	166	260	309	822	406	83	113	–	–	–	–	–	–	2,159	2.8	49.8	
Percentage	–	–	–	–	–	–	9.7	3.2	5.2	34.7	27.9	0.7	2.2	–	–	–	–	–	–				
1946																							
Age	–	–	–	–	–	–	–	–	III	IV	V	VI	VII	–	–	–	–	–	–				
Pounds	–	–	–	–	–	–	–	–	12	648	506	165	–	–	–	–	–	–	–	1,331	1.7	30.7	
Percentage	–	–	–	–	–	–	–	–	0.2	27.4	34.7	1.4	0.2	–	–	–	–	–	–				
1947																							
Age	–	–	–	–	–	–	–	–	II	III	IV	V	VI	–	–	–	–	–	–				
Pounds	–	–	–	–	–	–	–	–	24	78	244	248	87	–	–	–	–	–	–	681	0.9	15.7	
Percentage	–	–	–	–	–	–	–	–	0.4	3.3	16.8	21.	1.7	–	–	–	–	–	–				
1948																							
Age	–	–	–	–	–	–	–	–	–	II	III	IV	V	VI	VII	VIII	–	X	–				
Pounds	–	–	–	–	–	–	–	–	–	24	106	1,179	206	25	13	21	–	1	–	1,575	2.0	36.4	
Percentage	–	–	–	–	–	–	–	–	–	1.0	7.3	10.0	4.0	0.5	0.3	0.3	–	0.8	–				

(*Continued*)

TABLE XIV. Estimated contributions (thousands of pounds) of different year-classes of blue pike to the fall fishery of Lake Erie 1941–59.[a] — (*Concluded*)

	Year of capture																			Total for year-class		
Year-class	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	Pounds	Percentage of 1941–59 total	Percentage of 1941–59 mean
1949																						
Age	–	–	–	–	–	–	–	–	–	I	II	III	IV	V	VI	VII	VIII	–	X			
Pounds	–	–	–	–	–	–	–	–	–	12	81	9,737	3,962	1,708	585	279	21	–	–	16,385	21.0	378.2
Percentage	–	–	–	–	–	–	–	–	–	0.5	5.6	82.6	76.9	33.9	13.5	3.9	2.3	–	2.0			
1950																						
Age	–	–	–	–	–	–	–	–	–	–	–	II	III	IV	V	VI	VII	VIII	–			
Pounds	–	–	–	–	–	–	–	–	–	–	–	377	689	1,476	1,182	222	14	7	–	3,967	5.1	91.6
Percentage	–	–	–	–	–	–	–	–	–	–	–	3.2	13.3	29.3	27.3	3.1	1.5	4.5	–			
1951																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	II	III	IV	V	VI	VII	VIII			
Pounds	–	–	–	–	–	–	–	–	–	–	–	–	82	660	961	115	48	14	–	1,880	2.4	43.4
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	1.6	13.1	22.2	1.6	5.1	9.3	7.0			
1952																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	I	II	III	IV	V	VI	VII			
Pounds	–	–	–	–	–	–	–	–	–	–	–	–	6	1,119	987	158	19	17	1	2,307	3.0	53.2
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	0.1	22.2	22.8	2.2	2.0	10.8	15.2			
1953																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	–	I	II	III	IV	V	VI			
Pounds	–	–	–	–	–	–	–	–	–	–	–	–	–	50	390	100	27	20	–	587	0.7	13.5
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	–	1.0	9.0	1.4	2.9	12.8	11.1			
1954																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	–	–	I	II	III	IV	V			
Pounds	–	–	–	–	–	–	–	–	–	–	–	–	–	–	213	6,098	304	37	–	6,653	8.5	153.6
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4.9	85.1	32.7	24.1	11.6			
1955																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	I	II	III	IV			
Pounds	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	173	491	56	2	722	0.9	16.7
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.4	52.6	36.1	37.8			
1956																						
Age	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	I	II	III			
Pounds	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	2	1	11	–	–
Percentage	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.9	1.6	14.9			
Total	183	1,234	6,281	8,756	5,159	1,772	1,716	8,110	5,946	2,368	1,455	11,789	5,145	5,038	4,331	7,166	933	154	4	78,076		

[a]Year-class contributions less than 500 pounds and percentages less than 0.05 are not recorded.

[b]Since contributions of only the 1939 and 1940 year-classes were estimated for 1941 and 1942, and the 1938 year-class contribution was omitted in 1943, the only year it appeared in the samples, estimated contributions in 1941 and 1943 are less than the total production in those years and percentages do not equal 100; age-group I (1

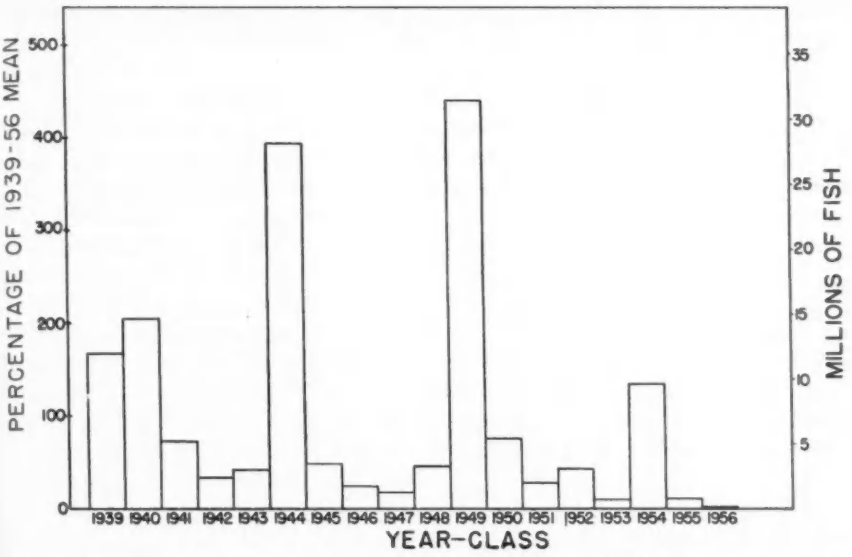

FIG. 7. Contributions of various year-classes of blue pike to the fall fishery of Lake Erie in 1941–59, expressed as total numbers and as percentage of the mean for year-classes 1939 to 1956.

when the marked improvement in growth rate increased the weight of fish in the various age-groups.

That fast growth was responsible in the later years for more rapid removal of young fish by the fishery is best shown by year-classes 1954–56. The contribution of these year-classes to the fishery was during the period of accelerated growth in 1955 and later years. Both year-classes were most abundant as age-groups I and II and few were older than age-group III.

EFFECT OF CHANGES IN ABUNDANCE ON THE FISHERY

Most of the stronger year-classes of blue pike contributed about half or more of their total yield (in pounds) to the fall fishery during a single season. These strong year-classes, the percentage of the total weight contribution of each during its peak season, and the age-group and year in which this percentage was taken were: 1939—54.6%, IV, 1943; 1940—53.8, IV, 1944; 1944—47.3, IV, 1948; 1949—59.4, III, 1952; and 1954—91.7, II, 1956. In numbers of fish, the total production for the peak fall season of each of these five year-classes amounted to 44.3% (56.9 million fish) of the total fall production (128.4 million) for the 18 year-classes in 1941–59.

The beginning or end of a period of heavy contribution of a year-class, as indicated by the Ohio trap-net fishery, sometimes was remarkably abrupt. The 1949 year-class, for example, yielded an average of 1028 fish per 10 trap-net lifts in the fall of 1952, as compared with 29 in the fall of 1951 (Table XV).

[a] Year-class contributions less than 500 pounds and percentages less than 0.05 are not recorded.
[b] Since contributions of only the 1939 and 1940 year-classes were estimated for 1941 and 1942, and the 1938 year-class contribution was omitted in 1943, the only year in question in the estimated contributions in 1941 and 1943 are less than the total production in those years and percentages do not equal 100; age-group I (1

TABLE XV. Numbers of blue pike of different year-classes caught per 10 trap-net lifts in Ohio in the fall, 1948–56. (Catches less than 0.5 fish are excluded.)

	Year-class															
Year	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956
1948	1	2	20	813	38	–	–	–	–	–	–	–	–	–	–	–
1949	–	2	18	738	61	4	4	–	–	–	–	–	–	–	–	–
1950	–	1	5	95	91	36	5	2	6	–	–	–	–	–	–	–
1951	–	–	–	4	31	70	57	27	29	–	–	–	–	–	–	–
1952	–	–	–	–	1	4	20	116	1028	46	–	–	–	–	–	–
1953	–	–	–	–	–	–	4	26	562	101	19	5	–	–	–	–
1954	–	–	–	–	–	–	–	1	121	138	62	138	3	–	–	–
1955	–	–	–	–	–	–	–	1	14	30	42	63	40	56	–	–
1956	–	–	–	–	–	–	–	–	3	4	2	2	8	624	30	–
1957	–	–	–	–	–	–	–	–	1	–	1	–	1	18	43	2
1958	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1

Sharp declines in fall catch were shown by the 1944 year-class in 1950 (a drop from 738 to 95 per 10 trap-net lifts), the 1949 year-class in 1954, and the 1954 year-class in 1957.

The short periods of high abundance and the sudden disappearance of strong year-classes of blue pike from the fishery inflicted severe hardships on Lake Erie commercial fishermen. The purchase of gear, maintenance of vessels, and employment of fishermen were sometimes complex and frustrating because of the constantly changing catches. Fishermen not only were required to adjust fishing operations to sudden changes in abundance, but often were faced with glutted markets and low prices.

The average price per pound of blue pike landed from 1945 through 1958 was 22.2 cents and ranged from 11.1 to 27.2 cents. Significantly, changes in production of New York, Ohio, and Pennsylvania were related inversely ($r = -0.94$; $p = 0.001$; df $= 40$) to changes in average price per pound in these states during 1945–58. Since the market for blue pike was supplied almost entirely by fish from Lake Erie, prices of blue pike were controlled largely by the volume of production in that lake.

The collapse of the blue pike fishery forced most fishermen to seek lower priced species, such as yellow perch (*Perca flavescens*), white bass (*Roccus chrysops*), freshwater drum (*Aplodinotus grunniens*), and smelt (*Osmerus mordax*). Other fishermen were forced out of business.

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The Teeth of Lampreys (Petromyzonidae): Their Terminology and Use in a Key to the Holarctic Genera[1]

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INTRODUCTION

The taxonomy of lampreys (Class Petromyzones, Berg, 1940) is based principally on the arrangement of the teeth. The "teeth" of lampreys are not identical with the true teeth of other vertebrates. They are hollow, stratified corneous cones, or sheaths, covering an axial papilla of the dermis. For further information on the structure of lamprey teeth, see Warren (1902) and Bridge (1932). Another peculiarity of lamprey teeth, at least in the parasitic species, is the periodic replacement of the corneous sheaths. Details of this replacement are given by Ivanova-Berg (1933), Hubbs and Trautman (1937, p. 29–34), Berg (1948, p. 51), Fontaine (1958, p. 73), Vladykov and Mukerji (1961), and Sterba (1962, p. 275).

Although the terminology of the different types of teeth is well established, there is no uniformity in its usage, particularly in popular works. Eddy (1957, p. 28–34) in describing lampreys stated that "the funnel is lined with cornified spines called teeth." He characterized *Petromyzon marinus* as having "more than 3 radiating rows of teeth, 4 or more teeth in each row on each side of opening in buccal funnel." Clemens and Wilby (1961, p. 27, 68) stated that in *Entosphenus tridentatus* the mouth is surrounded by a large, circular horny sucking disc, with horny plates as follows: (a) marginal, (b) supraoral, (c) lateral, (d) infraoral, (e) supraoral bar, (f) infraoral bar, and (g) lingual.

The English terminology for lamprey teeth was elaborated about 100 years ago by Günther (1870, p. 499–509). He used the expressions *maxillary lamina* instead of *supraoral lamina*, and *mandibulary lamina* instead of *infraoral lamina*. We owe our modern terms mainly to Regan (1911), Creaser and Hubbs (1922), Berg (1931), Holly (1933), Hubbs and Trautman (1937), Vladykov (1949), and Vladykov and Follett (1965).

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The present authors feel that the current terminology is rather involved and often not uniformly applied. We propose more simplified terms without sacrificing the exact meaning and shall illustrate their usage in all known Holarctic genera of lampreys.

POSITION OF TEETH

Teeth that are found on the sucking disc of lampreys may be unicuspid, bicuspid, or tricuspid. In general, in parasitic lampreys, particularly during the active feeding period, the teeth are sharp; in nonparasitic species the teeth are usually rather blunt. In *Caspiomyzon wagneri* the teeth are blunt and unsuitable for parasitic feeding. Although the details of their feeding habits are unknown, these lampreys are migratory and spend some time in the Caspian Sea prior to their return to native streams for spawning.

The sucking disc of any lamprey can assume a nearly circular shape. The terminology of the teeth is based on their particular position, which may be schematically illustrated by placing them in three circles: *outer*, *middle*, and *inner* (Fig. 1; modified after Holly, 1933, p. 10).

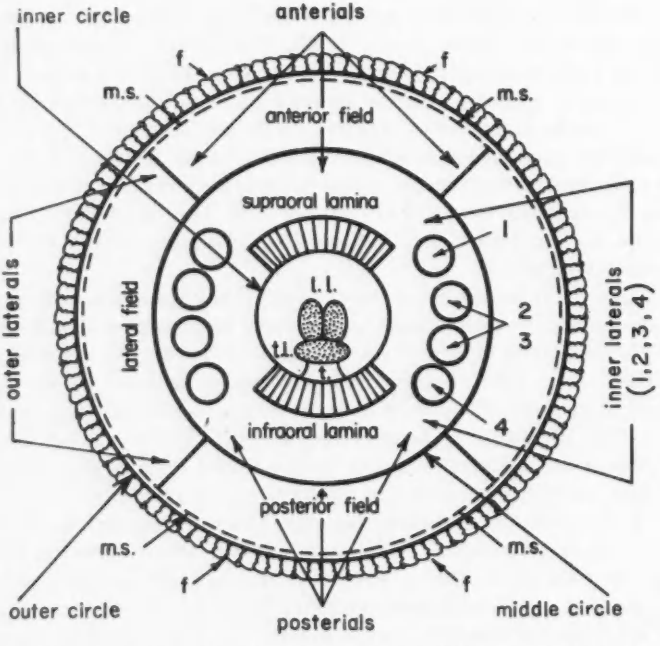

FIG. 1. The disc and dentition of a hypothetical lamprey of the family Petromyzonidae, modified after Holly (1933). The abbreviations are as follows: f.– *oral fimbriae* or leathery marginal appendages; l.l.– *longitudinal lingual laminae*; m.s.– *marginal series* of small teeth known as *marginals*; t.– *tongue* with three *lingual laminae*; t.l.– *transverse lingual lamina*.

There are four fields on the disc: *anterior*, *posterior*, and *two laterals*. Each of these fields has teeth of particular significance.

Outer Circle

The outer circle corresponds to the *marginal membrane* of the disc, outside of which is a fringe of *oral fimbriae*, or leathery marginal appendages, some of which are sensory.

Inward from the marginal membrane is a single circular row of small teeth, known as *marginals*, or teeth of the marginal series. They are present in lampreys of all species and hence, they have no taxonomic significance.

Inward from the marginals are somewhat larger teeth: *anterials*, on the anterior field; *posterials*, on the posterior field; and *outer laterals*, or *exolaterals*, on the lateral fields. In some genera, teeth of the anterior and posterior fields may occur on both sides of the middle circle, as shown in Fig. 1. Teeth on all four fields are intermediate in size between the marginals and the inner laterals.

The anterials are of little importance from the taxonomic viewpoint, except for their numbers. The posterials are absent only in the genus *Lampetra*.

The outer laterals are on the lateral fields, between the outer and middle circles of the scheme. These teeth are absent only in the genera *Lampetra*, *Lethenteron*, and *Entosphenus*.[2]

Middle Circle

Within the middle circle of the scheme are the most specialized and most important teeth. Above the oesophageal opening is the *supraoral lamina* (Fig. 1–3) which, in some genera, is reduced to a tooth with 1–4 cusps (2 cusps in Fig. 4). Below the oesophageal opening is the *infraoral lamina*.

On each side of the oesophageal opening are the *inner laterals*, or *endolaterals* which are much larger than outer laterals. The number of the former and their structure are of great taxonomic importance. There are 3 or 4 on each side; in *Ichthyomyzon* there are sometimes 5 (Hubbs and Trautman, 1937, p. 30, 32). The inner laterals (or some of them) may be unicuspid, bicuspid, or tricuspid. With rare exceptions, the inner laterals are equal in number on each side, and are symmetrical in position. Hence, the number of inner laterals on one side only of the disc is sufficient to characterize a lamprey genus.

Hubbs and Trautman (1937, p. 30) proposed a new term for the innermost disc teeth, namely the *circumoral row*.[3] In this row they include: (a) the inner laterals, (b) 1 or more anterials, and (c) several posterials. According to them, the basic number of circumorals in the genus *Ichthyomyzon* seems to be 15, including 1 anterial, 4 inner laterals on each side, and 6 posterials. We do not consider the circumoral row useful in other genera.

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[2]Berg (1931, p. 91) erroneously stated that in the genus *Entosphenus* outer lateral teeth are present.

[3]Vladykov and Follett (1958, 1965) used the term *circumorals* synonymously with *inner laterals*.

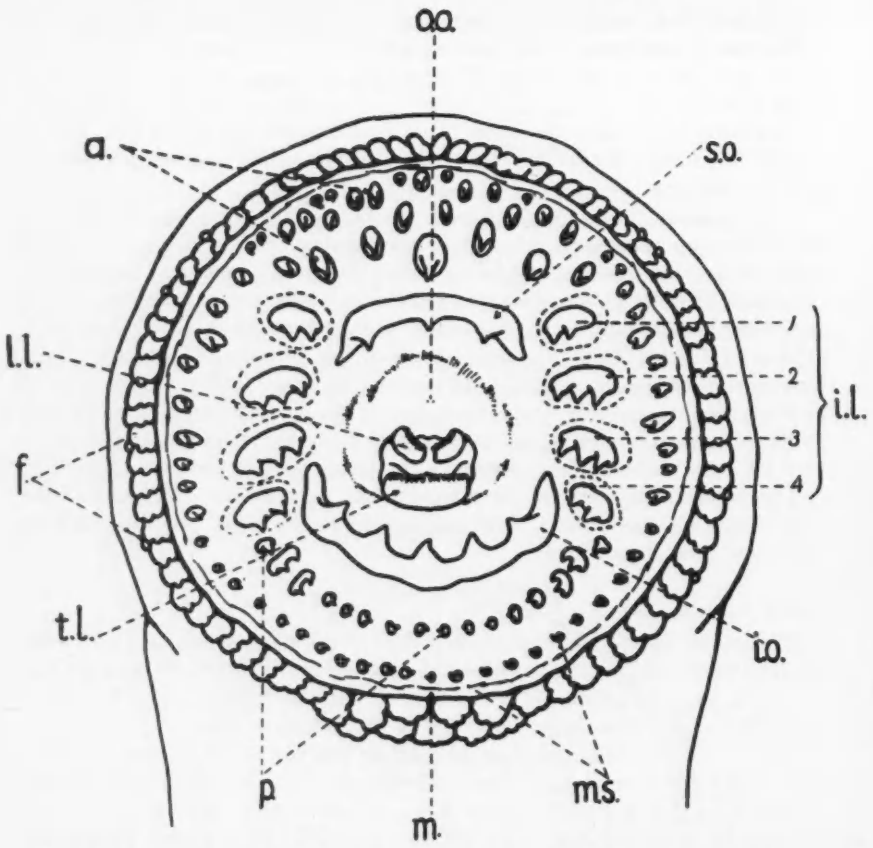

FIG. 2. Schematic drawing of the disc and dentition of a Pacific lamprey, *Entosphenus tridentatus*, modified from Vladykov and Follett (1958). Abbreviations used in this drawing are as follows: a.– *anterials*, or teeth of the *anterior field*; f.– *oral fimbriae*, or leathery marginal appendages; i.l.– four *inner laterals*, or *endolaterals*; i.o.– *infraoral lamina*; l.l.– *longitudinal lingual laminae*; m.– *marginal membrane*; m.s.– *marginals*, or *marginal series*; o.o.– *oesophageal opening*; p.– *posterials*, or teeth of the *posterior field*; s.o.– *supraoral lamina*, with a strong cusp on the middle of the bridge, and one cusp at each end; t.l.– *transverse lingual lamina*. NOTE: Some *posterials* are bicuspid; the *outer laterals* (or *exolaterals*) are absent.

INNER CIRCLE

Located in the inner circle of the scheme is the tongue, on which there are three *lingual laminae*, each carrying a row of *lingual cusps:* a single *transverse lamina* and two *longitudinal laminae*, whose cusps could be called *transverse linguals* and *longitudinal linguals*, respectively. The terms, transverse and longitudinal lingual laminae, were proposed with good reason by Hubbs and Trautman (1937, p. 32) to replace, respectively, *anterior* and

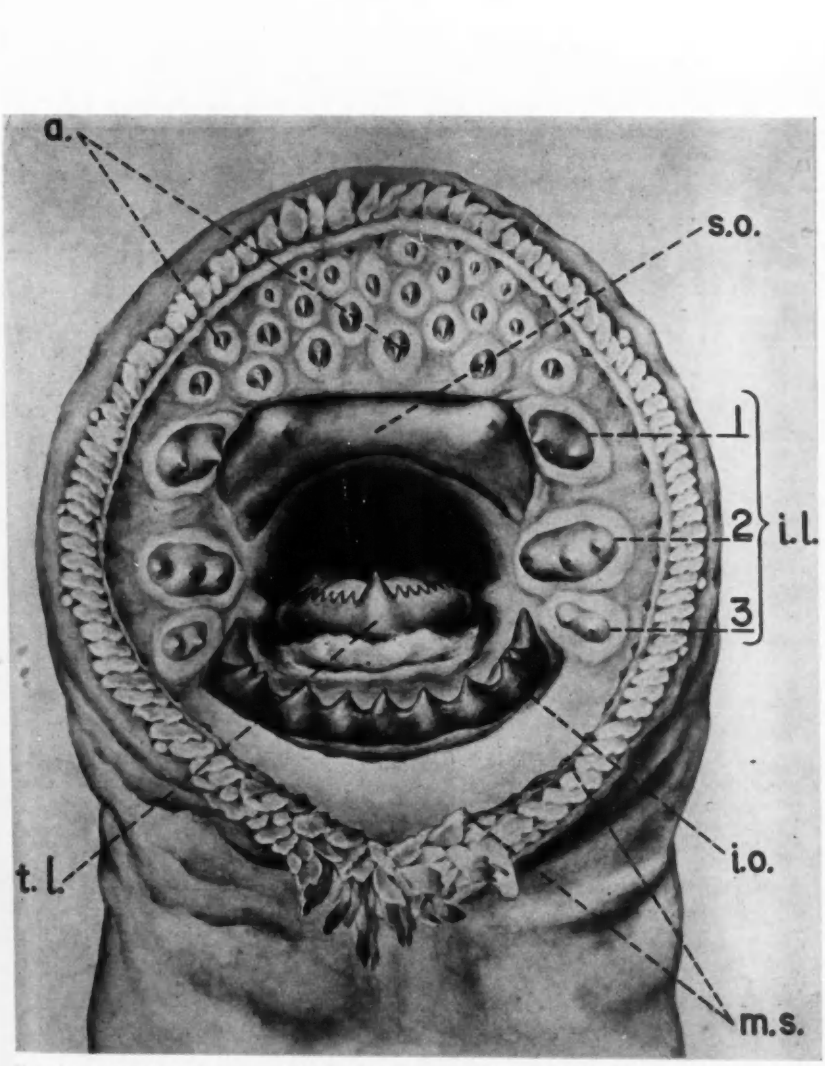

FIG. 3. Disc of *Lampetra ayresii*, after Vladykov and Follett (1958). For an explanation of the abbreviations see Fig. 2. NOTE: Absence of the *outer laterals* (or *exolaterals*) and *posterials*.

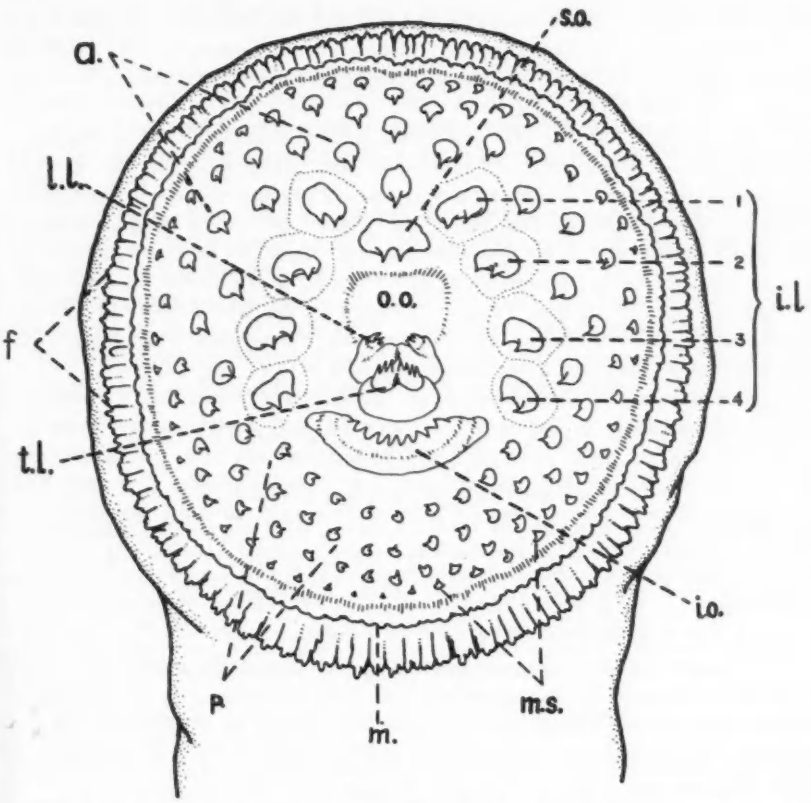

FIG. 4. Schematic drawing of the disc and dentition in the landlocked sea lamprey, *Petromyzon marinus*, modified from Vladykov and Mukerji (1961). For an explanation of the abbreviations see Fig. 2. NOTE: There are numerous teeth on all four fields; the *supraoral lamina* (s.o.) has no bridge, but is represented by *supraoral cusps*.

posterior laminae, which had been in common use. From the taxonomic viewpoint, the transverse lingual lamina is the more important one.

DESCRIPTION OF TEETH

MARGINALS

These small teeth have no taxonomic importance.

TEETH OF THE FOUR FIELDS

The teeth in the fields differ in their taxonomic value and hence must be treated separately.

(a) *Anterior field.*—In *Caspiomyzon*, *Petromyzon*, and *Ichthyomyzon* the anterior disc teeth or anteriors are numerous, close-set, and arranged in curvilinear radiating rows. In *Eudontomyzon* these teeth are villiform, rather

small, numerous, sharp in parasitic species, and less close-set, but also arranged in radiating rows. In *Entosphenus*, *Tetrapleurodon*, *Lampetra*, and *Lethenteron*, the anterior disc teeth are well spaced, and not arranged in curvilinear radiating rows.

(b) *Posterior field.*—The posterials are absent only in *Lampetra*. In *Caspiomyzon*, *Petromyzon*, *Ichthyomyzon*, and *Eudontomyzon*, the posterials are numerous, in 3 or 4 curved rows, and all are unicuspid. In *Entosphenus*, *Tetrapleurodon*, and *Lethenteron* these teeth are in a single row, and unicuspid; however, in *Entosphenus* some of these teeth are bicuspid

(c) *Lateral fields.*—Outer laterals or exolaterals are absent in *Entosphenus*, *Lampetra*, and *Lethenteron*. They are present in the lateral fields in *Tetrapleurodon*, in 1 or 2 curved rows. In *Caspiomyzon*, *Petromyzon*, *Ichthyomyzon*, and *Eudontomyzon*, they are more numerous, and in 3 or 4 rows.

Inner laterals or endolaterals are particularly important in separating genera of lampreys. In *Lampetra*, *Lethenteron*, and *Eudontomyzon* there are 3 inner laterals on each side of the oesophageal opening; in *Caspiomyzon*, *Petromyzon*, *Ichthyomyzon*, *Entosphenus*, and *Tetrapleurodon*, there are 4. The inner laterals may be unicuspid, bicuspid, tricuspid, or a combination of the three.

LAMINAE

(a) *Supraoral lamina.*—There are two distinct types:

(i) Lamina with a cusp at each end, the cusps separated by a bridge (Fig. 3). In *Lethenteron*, *Eudontomyzon*, and *Tetrapleurodon*, but not in *Lampetra*, one or more smaller cusps may occur on the middle of the bridge. In *Entosphenus*, the median cusp is nearly as strong as those at each end of the bridge (Fig. 2).

(ii) Instead of a lamina there is a single tooth with one or several (2–4) cusps not separated by a bridge (Fig. 4). This tooth should be called *supraoral*. In *Caspiomyzon*, *Petromyzon*, and *Ichthyomyzon*, the supraorals are of this type.

(b) *Infraoral lamina.*—This structure has little taxonomic significance. In most genera, it usually has 7–11 cusps, which typically are all unicuspid. In some genera, the outermost cusps may be bicuspid. In *Caspiomyzon* and *Entosphenus*, there are usually only 5 infraoral cusps.

(c) *Lingual laminae.*—The longitudinal lingual laminae in all lampreys are more or less similar, but the number of their cusps may vary with the genus. These laminae on the tongue are difficult to examine. The transverse lingual lamina, the principal rasping organ of parasitic species, is more easily accessible. The arrangement of its cusps varies with the genus. The cusps are located on the anterior, denticulate ridge of the transverse lingual lamina. In all lampreys, the middle cusp (occasionally two) is somewhat larger than the others; it is greatly enlarged only in *Lampetra*, *Lethenteron*, and *Eudontomyzon*.

In general, the following five main types of transverse lingual lamina can be distinguished:

(i) Bilobed, strongly bent inward along a longitudinal median groove, and with strong cusps on the denticulate ridge, as in *Petromyzon* (Fig. 4).

(ii) Bilobed, without a median groove, and with numerous small cusps on the denticulate ridge, as in *Ichthyomyzon* (see Hubbs and Trautman, 1937; Fig. 3).

(iii) Not bilobed, slightly convex on the outer surface, and with the median cusp of the denticulate ridge strongly enlarged, as in *Lampetra*, *Lethenteron*, and *Eudontomyzon* (Fig. 3).

(iv) Not bilobed, the median cusp not strongly developed, the denticulate ridge nearly straight, comblike, as in *Entosphenus* and *Tetrapleurodon* (Fig. 2).

(v) Not bilobed, without a strong median cusp on the denticulate ridge; all cusps blunt and weakly developed, as in *Caspiomyzon*.

KEY TO THE GENERA OF HOLARCTIC LAMPREYS
(Family PETROMYZONIDAE)

Based Exclusively on Characters of the Teeth

1a. Anterials, posterials, and outer laterals numerous, close-set in curvilinear radiating rows; instead of a supraoral lamina, a single supraoral tooth, unicuspid, or with 2–4 cusps not separated by a bridge; 4 (5, the rare exception in *Ichthyomyzon*) inner laterals on each side of the oesophageal opening; transverse lingual lamina bilobed or not, without greatly enlarged median cusp.

2a. All teeth blunt, inner laterals unicuspid; transverse lingual lamina not bilobed, and without a longitudinal median groove. Caspian Sea and tributaries.

Caspiomyzon Berg, 1906

2b. All teeth sharp (at least in parasitic species), inner laterals unicuspid or bicuspid; transverse lingual lamina bilobed.

3a. Inner laterals bicuspid; transverse lingual lamina strongly bent inward along longitudinal median groove and with 14–18 large cusps. Both sides of North Atlantic Ocean and Mediterranean Sea areas.

Petromyzon Linnaeus, 1758

3b. Inner laterals unicuspid or bicuspid; transverse lingual lamina without a median groove and with many (about 30) small cusps. Fresh waters of eastern North America.

Ichthyomyzon Girard, 1858

1b. Anterials, posterials, and outer laterals (if present) not in curvilinear radiating rows and, with the exception of *Eudontomyzon*, not numerous; supraoral lamina with a cusp at each end, the cusps separated by a bridge; 3 or 4 inner laterals on each side of the oesophageal opening; transverse lingual lamina not bilobed, with or without greatly enlarged median cusp.

4a. Four inner laterals; denticulate ridge of transverse lingual lamina comblike without greatly enlarged median cusp. Posterials in a single curved row.

5a. Supraoral lamina with a strong cusp on the middle of the bridge; anterior and posterior (1st and 4th) inner laterals bicuspid, middle two (2nd and 3rd) tricuspid; outer laterals absent. Pacific drainage of North America.[4]

Entosphenus Gill, 1863[5]

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[4]Although *Entosphenus tridentatus* (Gairdner) is occasionally taken off Hokkaido, it is not definitely known to spawn in Japan.

[5]American Fisheries Society (1960, p. 6) listed the scientific name of the Pacific lamprey as *Lampetra tridentata* (Gairdner) instead of *Entosphenus tridentatus*.

5b. Supraoral lamina with or without one or more minute cusps on the middle of the bridge; all four inner laterals bicuspid, or the middle two tricuspid; 1 or 2 curved rows of outer laterals. Western Mexico (Rio Lerma basin).

Tetrapleurodon Creaser and Hubbs, 1922

4b. Three inner laterals; denticulate ridge of transverse lingual lamina with greatly enlarged median cusp; posterials and outer laterals present or absent.

6a. Posterials and outer laterals absent; anterior and posterior inner laterals typically bicuspid, the middle tricuspid. Europe and North America.

Lampetra Gray, 1853[6]

6b. Posterials present; outer laterals present or absent; all three inner laterals bicuspid.

7a. Teeth of disc not numerous and non-villiform; posterials in a single curved row; outer laterals absent. Eurasia in Arctic Ocean drainage, from White Sea to North Pacific Ocean, and North America.

Lethenteron Creaser and Hubbs, 1922

7b. Teeth of dics numerous and villiform; 2–4 curved rows of posterials and outer laterals. Black and Baltic sea basins, and Korea (Yalu River).

Eudontomyzon Regan, 1911

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Age and Growth of American Plaice (*Hippoglossoides platessoides*) in the Newfoundland Area of the Northwest Atlantic[1]

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ABSTRACT

Growth curves of American plaice (*Hippoglossoides platessoides* Fabricius) from the Grand and St. Pierre banks and the areas east of Newfoundland are presented. Ages were determined using otoliths from random samples collected by research vessels in the spring and summer during 1957–63.

For the localities sampled, American plaice on the southern half of the Grand Bank are the largest and the St. Mary's Bay population the smallest at comparable ages. A positive association was found between the sizes at ages 5 and 15 for the various localities and the probable bottom temperatures.

Samples of otoliths from St. Mary's Bay indicated that the greatest growth occurs during the May–November period.

Year-class dominance was noted for St. Mary's Bay, but not for other areas.

INTRODUCTION

The purpose of this paper is to give the growth curves of American plaice (*Hippoglossoides platessoides*) for the Newfoundland area of the Northwest Atlantic and to show how the growth of this species is related to bottom temperatures and probably also the availability of food. The age composition of the stocks is also discussed.

Previously published work on the age composition and growth of this species in the Northwest Atlantic included growth curves and age distributions for the southern part of the Gulf of St. Lawrence by Huntsman (1918) and Powles (1965), and by Yanulov (1962) for the area off Labrador and east of the Grand Bank (ICNAF Subareas 2 and 3).

The largest commercial concentrations of American plaice in the Northwest Atlantic occur on the seaward side of the Grand Bank (Fig. 1) which is in contact with the cold Labrador Current in 40–100 fath (73–183 m) on the northern and northeastern slopes and in 40–150 fath (73–274 m) on the eastern slope. Fishing rarely occurs deeper than 85 fath (155 m) on the southeast and southern portions of the Grand Bank with the principal concentrations usually at 35–60 fath (64–110 m). Some American plaice are caught also in the Avalon Channel between the northern half of the Grand Bank and the coast of Newfoundland.

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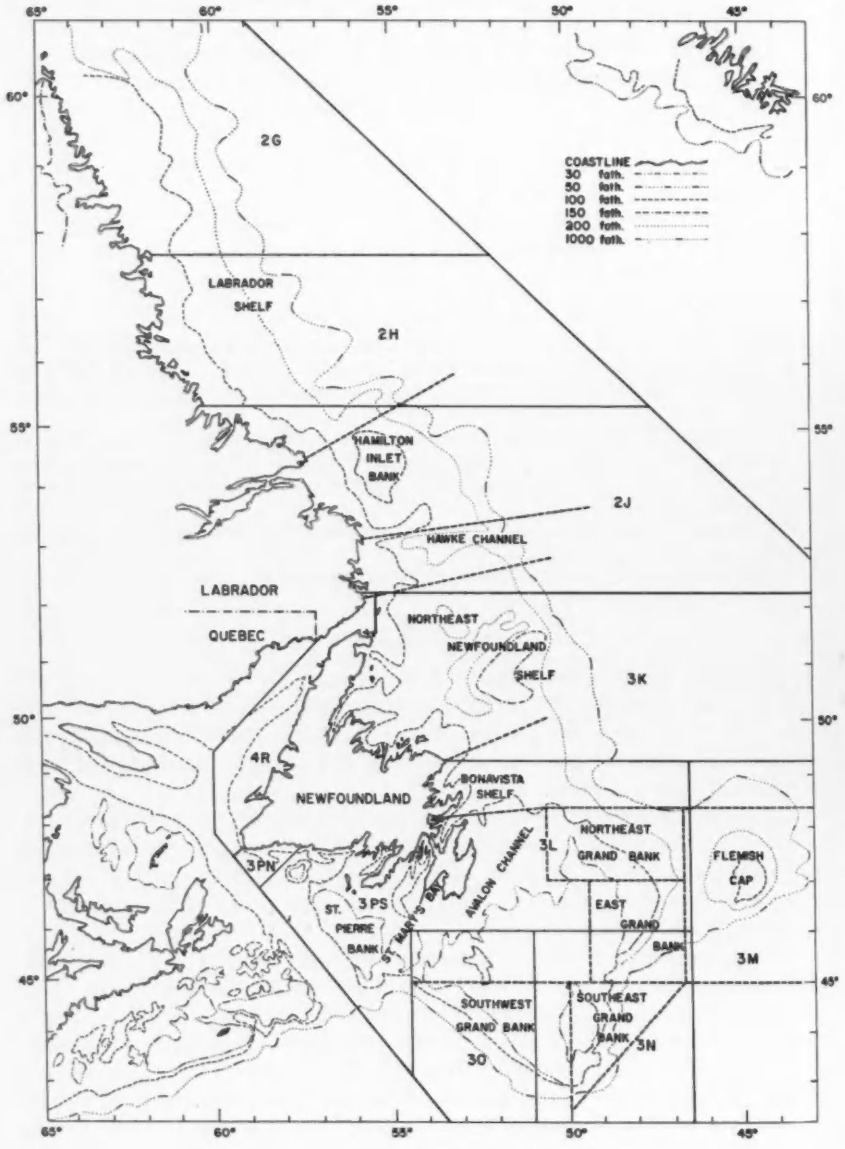

FIG. 1. Areas referred to in the text.

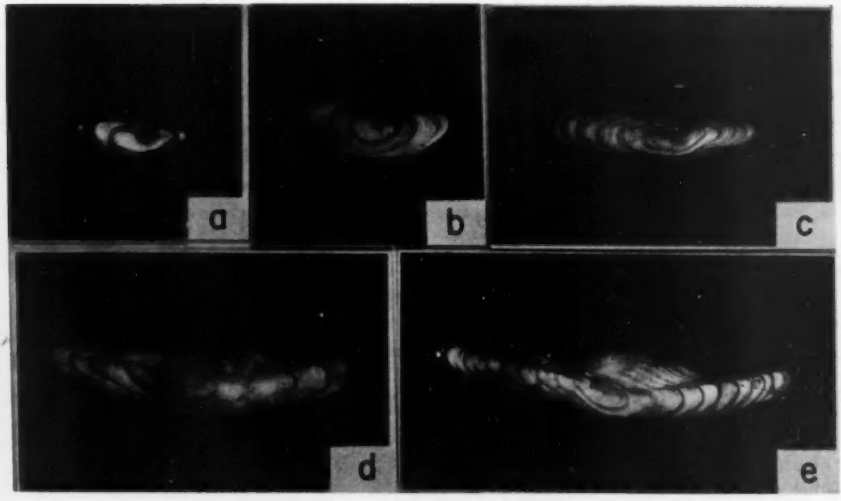

FIG. 2. Illustration of broken surfaces of American plaice otoliths. (a) 1+, 4.2 cm, St. Mary's Bay, September 1957; (b) 3+, 9.7 cm, St. Mary's Bay, September 1957; (c) 5+, 15 cm, St. Mary's Bay, October 1962; (d) 5, 26 cm, SW Grand Bank, April 1963; (e) 10+, 27 cm, St. Mary's Bay, June 1962. Magnification approx 10×.

Pitt — J. Fish. Res. Bd. Canada

In areas north of the Grand Bank and in the various bays around Newfoundland, plaice are usually caught in less than commercial quantities, although fairly large catches have been secured by research vessels on Hamilton Inlet Bank.

MATERIAL AND METHODS

The growth curves and age-distribution graphs were prepared from samples collected during regular survey cruises by research vessels operated by the Fisheries Research Board of Canada at St. John's, Nfld. The gear used was the otter trawl with the codend lined with $\frac{1}{2}$–$1\frac{1}{8}$-inch nylon netting. The tows were almost always of 30 min duration.

A fraction of the catch from each set was sampled to obtain a length frequency and from these samples specimens were taken at random for a detailed study of age, sex, and maturity. When a catch from a particular set was small (up to 50 fish) usually the entire catch was examined. For all the St. Mary's Bay samples and also some of the other samples the specimens were brought in ice to the laboratory for detailed examination.

Approximately 17,000 pairs of otoliths, collected from April to August 1957–63, were used to calculate the average sizes at various ages for the different areas. The areas (Fig. 1) are similar to those used in previous papers (Pitt, 1963, 1966). The samples for a particular area were combined so that fish from a range of depths were sometimes included in the calculation of the average size and year-class distribution frequencies.

Because the otoliths from St. Mary's Bay were particularly suitable for age determination (Fig. 2), this locality was used as a sample area to follow the growth of certain year-classes and the formation of the zones on the otoliths. This area was sampled monthly or bimonthly during 1957 and 1958 and at least one sample was taken in 1959–61 and 1963.

The Southwest Grand Bank was sampled annually from 1957 to 1963 when the research vessels were engaged in haddock surveys with most of the samples coming from the southern part of this area. Other areas were not sampled on a regular basis.

Up to about ages 5–7 years male and female plaice grow at approximately the same rate (Fig. 5, 6, and 8), but since males mature earlier than the females (Pitt, 1966) it seems likely that energy is diverted at an early age from growth to reproduction so that the rate of growth of the male is reduced at an earlier age than in the female. Because of the greater range of ages for the female plaice in many of the comparisons between areas, only the growth curves of the females were used.

In presenting the year-class distribution (Fig. 13–15) there are two possible sources of error. The first is the fact that some samples were relatively small and may not be entirely representative of the population, and the second is the possibility of error in the interpretation of age from the otoliths, especially in the older fish.

Shrinkage of Iced Plaice

To determine the shrinkage of fish held in ice several groups of fish were measured at sea, stored in ice, and then measured again at the Station. Both measurements were by the same person to the nearest centimeter.

A straight line relationship was established between the two measurements as follows:

$$L = 0.2 + 1.006\ L_1$$

where L and L_1 are the fresh fish length and iced length in centimeters respectively.

The mean change in length was approximately 1%. This compares closely with the 1.4% shrinkage calculated by Lux (1960) for yellowtail flounder where the sizes ranged to 45.5 cm. For my experiments the largest fish were 65 cm.

Aging Methods

Ages were determined by examination of the sacculus otoliths which were removed from the fish and stored in envelopes. All except the smallest otoliths were broken in half (Fig. 2) and the pieces embedded in black modelling clay with the broken surface flush with the surface of the modelling clay. The surface of the otolith was moistened with 95% ethyl alcohol and the dark annual zones were interpreted using a stereoscopic microscope with blue reflected light. For whole otoliths difficulty was encountered in establishing the position of the first two or three annual zones, especially for the older fish, because of the thickness of the central part of the otolith.

Powles (1965) presented data from the Gulf of St. Lawrence on the recapture of tagged American plaice and also the consistency of strong and weak year-classes, which provide evidence of the validity of otoliths for the determination of age in this species. The year-class distribution from St. Mary's Bay (Fig. 13) and the annual cycle in the deposits at the edge of the otolith (Fig. 3 and 11) are presented here as evidence of the validity of the otolith method.

Calculation of the Growth Curves

Beverton and Holt (1957) showed that for certain problems in population dynamics it is useful to describe the growth of a particular species in mathematical terms. The expression that has been most widely accepted in recent years is that of von Bertalanffy (1938):

$$l_t = L_\infty\left[\ 1 - e^{-K(t-t_0)}\ \right]$$

where l_t is the length at age t (in years), $L\infty$ is the theoretical maximum length, K is a constant expressing the rate of change in the length increments with respect to t, and t_0 is the hypothetical age at zero length. The estimation of $L\infty$ by the usual method of the regression of length at age $t+1$ on length at age t (Walford, 1946) usually resulted in a poor fit of the von Bertalanffy

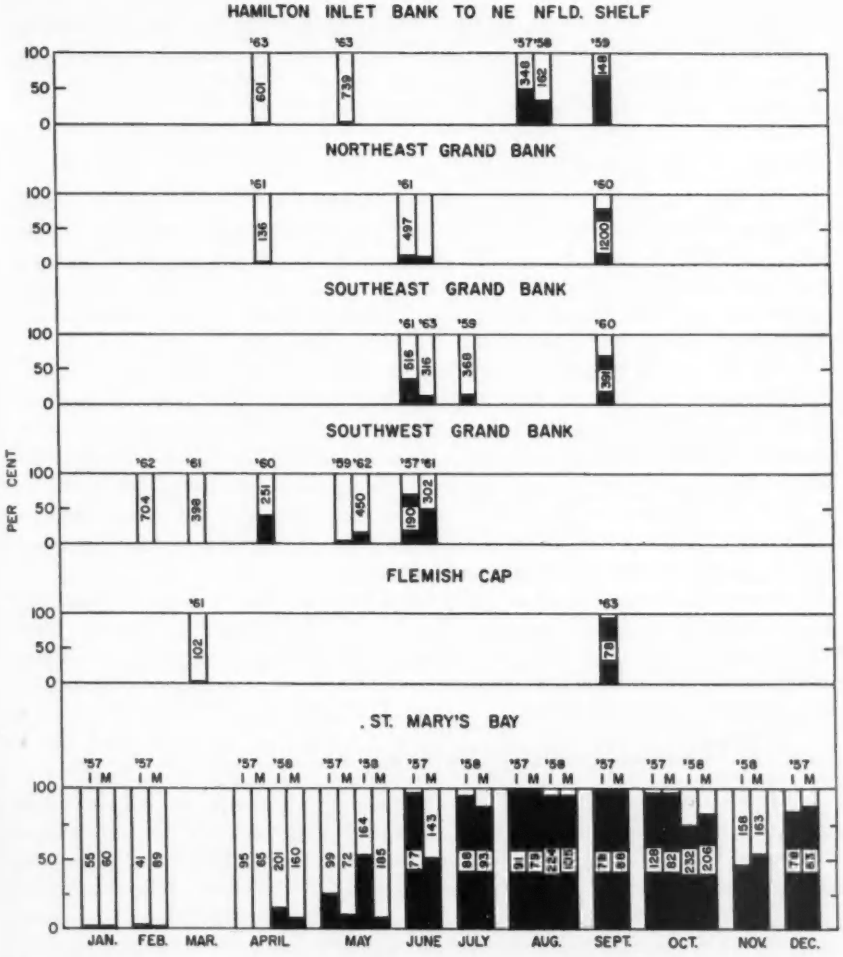

FIG. 3. Percentages of American plaice from various areas with otolith edges opaque (black bars): St. Mary's Bay, immature (I) and mature (M); other areas with all fish combined. The numbers of fish involved are shown and the years when the fish were caught.

equation so that the method suggested by Ricker (1958) was used. The von Bertalanffy equation has been widely accepted as an empirical description of growth and is presented as such in this investigation and no attempt was made to relate the various parameters of this equation to the physical environment.

The various growth curves were calculated from specimens taken over a number of years, during which fluctuations in temperature occurred and during which fish probably changed their depth location. Therefore, in relating

the growth of fish to the environmental temperature the figures used (Fig. 10) are observed averages and the probable temperature range for any given area. These temperatures were from data collected by research vessels operated by the St. John's Station during June–August 1959–63 (Fig. 4).

Interpretation of the Otolith Edge

The interpretation of the age of a fish from its otoliths is based on the formation of two zones each year, one opaque and one translucent. The opaque zone, which is usually the largest, is associated with the period of greatest growth of the otolith and the fish. The period of the year when these zones appear may vary between species and populations of the same species and there may also be variations within the same population.

The interpretation of the otolith edge was sometimes difficult especially in older fish where the individual zones were narrow. Difficulty was also encountered in determining the composition of the otolith edge during the transitional period between the two zones. This was particularly so in otoliths from fish caught during the period September–December, when the beginning of the translucent zone or the end of the opaque zone was not always clearly defined. Hence, the percentages of otoliths with opaque and translucent edges (Fig. 3) must necessarily be only approximate.

A greater percentage of otoliths from the St. Mary's Bay samples had opaque edges in April and May in 1958 than in 1957 (Fig. 3). This may have been caused by hydrographic differences since bottom temperatures during the spring of 1957 were about 2 C lower than at a comparable period in 1958 (Fig. 11C).

INFORMATION ON STUDY AREAS AND POPULATIONS

As previously stated the major commercial fishery for this species takes place along the seaward slope of the Grand Bank (Northeast, East, and Southeast Grand Bank, Fig. 1). However, in this paper, growth-curves are presented from all areas fished by research vessels operated by the St. John's Station.

Labrador Shelf to Bonavista Shelf (*Fig. 1*).— This area includes the shelves lying east of Labrador and northeast of Newfoundland. No widespread commercial concentrations of pläice were found in this area but some relatively good concentrations occur at certain localities. A few specimens were generally caught in most areas fished down to 250 fath (475 m). The largest concentrations occurred on Hamilton Inlet Bank, where a few catches of up to 5000 lb per hour were taken with a lined net at 90 fath (165 m) at –0.3 to 0 C.

During the summer, water below 0 C extends to 100 fath (183 m) in this area. Most of the sampling was during the early spring at 125–250 fath (229–457 m) with temperatures 0.5–3.0 C (Fig. 4, lines I and II). Although there could be seasonal migrations between shallow localities with low temperatures and the deeper localities (Pitt, 1966), for the area as a whole, American plaice generally live between 100 and 150 fath (183–274 m) in temperatures between –0.5 and 1.5 C.

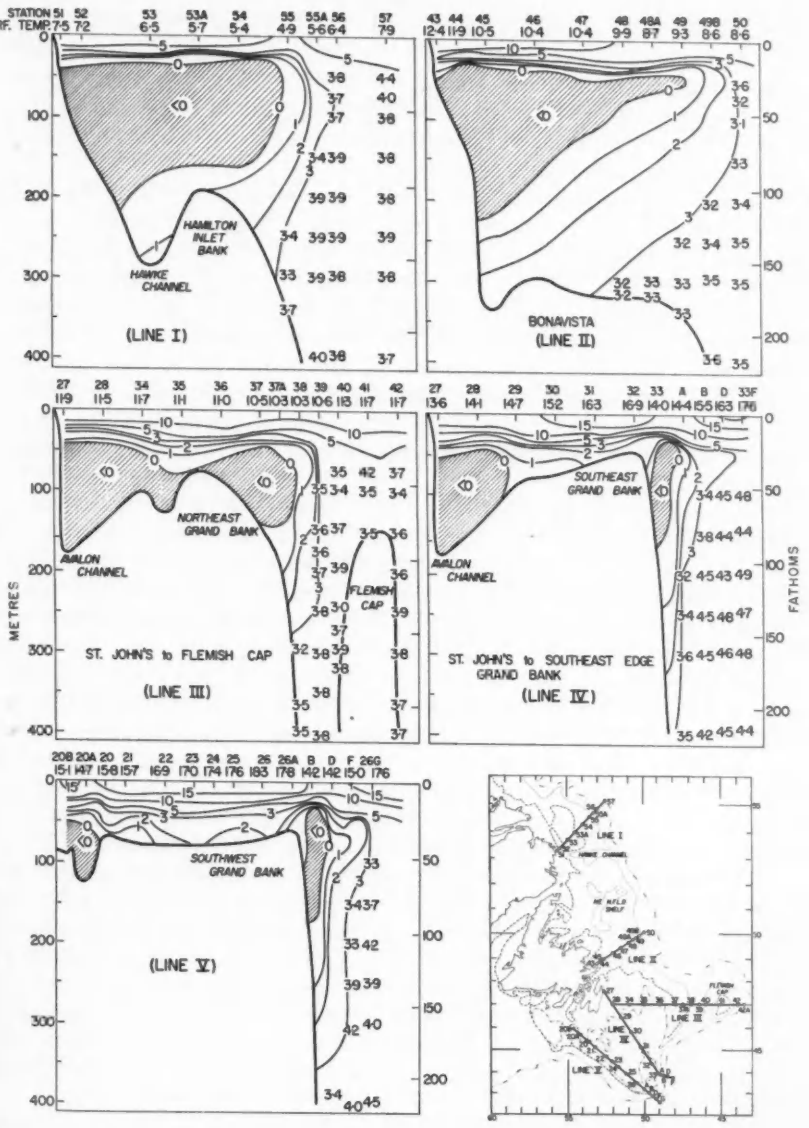

FIG. 4. Average temperature profiles for most of the study areas for July and August (1959–63) (adapted from May et al., 1965).

The Grand Bank (*Fig. 1*).— The slope of the Grand Bank to the north and northeast is gradual. Thus the distance between the 50-fath (91 m) and the 100-fath (183 m) contours is about 60 miles at the northern tip. The seaward

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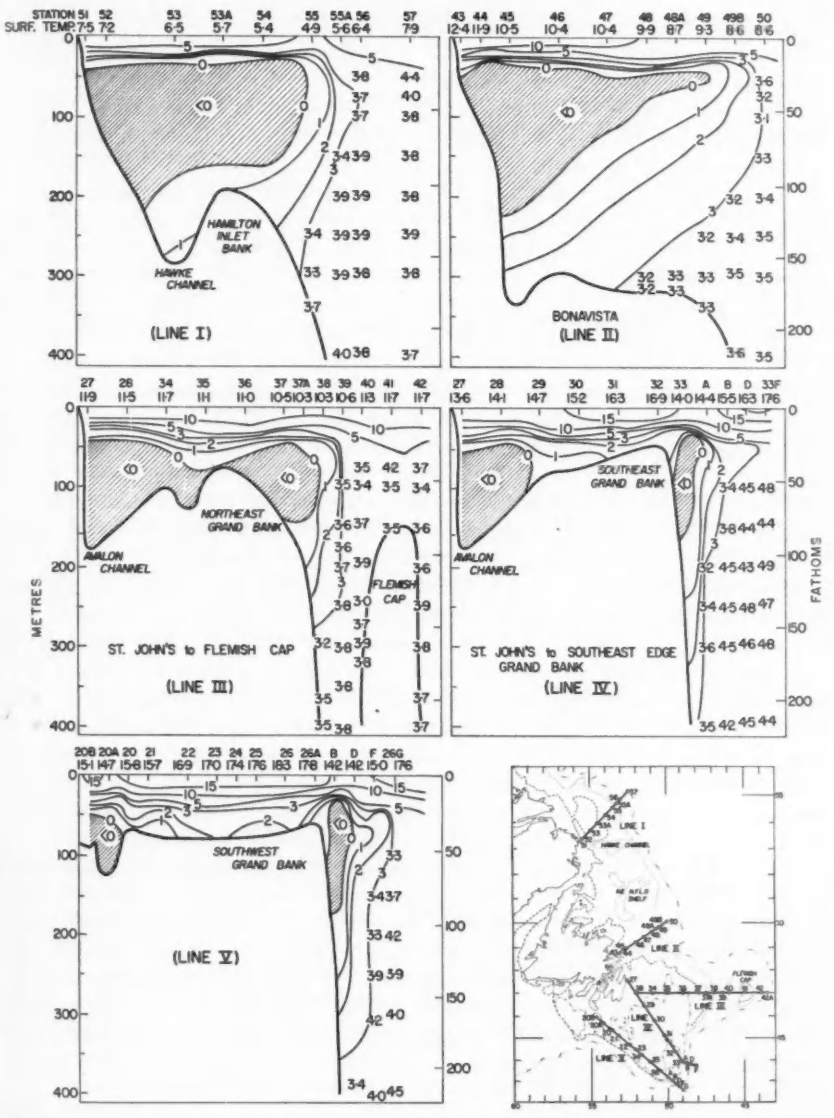

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slope of the bank gradually becomes steeper from north to south along the eastern slope until at about 45°30′N the 50- and 100-fath (91 and 183 m) contours are relatively close together.

The subdivision of the seaward slope of the Grand Bank into Northeast, East, and Southeast areas was partly arbitrary and in part based on the bottom configuration and its resulting environment.

Plaice on the Northeast Grand Bank are concentrated principally between 50 and 80 fath (91 and 140 m) in temperatures generally between –0.5 and 1.0 C. To reach higher temperatures they would have to seek depth usually below the 100-fath (183 m) contour which, in this area, would entail considerable movement. Small plaice (below 20 cm) were usually concentrated at 100 fath (183 m) on the north and northeast parts of the Grand Bank, where the temperatures were below 0 C, and also at 40–60 fath (73–110 m) where the temperatures were usually 0 to –1.5 C. Tagging of commercial size plaice (above 30 cm) revealed little movement of plaice to other localities (unpublished data, Fisheries Research Board of Canada, Biological Station, St. John's, Nfld.).

On the East Grand Bank the slope becomes steeper southward as previously noted. Tagging just north of 46°N indicated some movement to the north whereas plaice tagged at about 45°N tend to migrate, if at all, in a general southerly direction (unpublished data). American plaice in shallow depths along the eastern slope of the bank are subjected to approximately the same hydrographic conditions as those from the Northeast Grand Bank but, in the southerly part of the East Grand Bank between 45 and 46°N, fairly large concentrations were found at 100–125 fath (183–229 m) in temperatures 1–2 C. There was also some evidence from tagging and fishing surveys that American plaice tend to make seasonal migrations between shallow and deep water in this locality. Those in shallow water (40–50 fath, 73–91 m) were feeding on bottom invertebrates, but those in deeper water, especially in the southern half of this area, fed heavily on launce and capelin.

The heaviest concentrations of plaice on the Southeast Grand Bank were at the southern tail of the bank in 35–60 fath (64–110 m) and on the slope just east of the Southeast Shoal (Fig. 1). Some were also caught in relatively small quantities at 80–85 fath (146–229 m). Unlike the northern half of the bank, temperatures above 0 C were available during the summer and fall at shallow depths (50 fath, 91 m). Capelin and launce were found in most of the stomachs of plaice examined. Tagging returns (unpublished) indicate some movement to the northeast along the southeast slope but little migration to the west.

The Southwest Grand Bank supports a relatively small population of American plaice although commercial fishing occurs at the extreme southerly part of the location in 60–80 fath (110–146 m). The largest catches by research vessels were at 1–3 C.

Flemish Cap (*Fig. 1*).— This area is not fished commercially for American plaice. Bottom temperatures are high, usually about 3 C (Fig. 4, line III).

A von Bertalanffy growth curve was fitted for the females only because of the small age-range of male specimens collected. Vertebral averages indicate that this is a population discrete from those of the Grand Bank (Pitt, 1963).

St. Pierre Bank (*Fig. 1*).— Most of the samples were taken at 60–100 fath (110–183 m) at 0 to 3 C. This area is not fished commercially for plaice to any great extent.

St. Mary's Bay.— The bay is under the influence of the Labrador Current and the average bottom temperature ranges from –0.5 in March to 0.6 C in October. This bay and the adjoining area support a small population of plaice which is probably discrete from those of Grand Bank and St. Pierre Bank. Tagging returns (unpublished) indicate little movement from this bay. The assumption was therefore made that this is a local population.

GROWTH

Growth curves for the various areas described are presented in Fig. 5, 6, and 8, and comparisons are shown in Fig. 7 and 9.

Growth patterns for the Labrador to Bonavista Shelf areas are similar (Fig. 9A). The most northerly area, Labrador Shelf, has a slightly greater length-at-age, but the difference is not great.

The growth curves for the four Grand Bank populations show an increase in average length-at-age from north to south (Fig. 6 and 7). The growth rate of the Southwest Grand Bank population is one of the greatest for the whole area.

The Flemish Cap population has a very rapid initial growth rate (Fig. 8A and 9B) probably because of the high bottom temperatures which are prevalent in this area.

The growth curve for St. Pierre Bank plaice (Fig. 8B) is similar to that of the East Grand Bank populations.

Plaice from St. Mary's Bay were generally smaller in length at comparable ages than those of the other localities presented here (Fig. 8C and 9).

A positive relationship was found between bottom temperature and the average length at ages 5 and 15 for the different areas (Fig. 10). The relationship for the 15-year-olds from Flemish Cap (No. 6) can perhaps be explained by the fact that American plaice from this locality grow very rapidly in their early years but the rate of increase is reduced at a comparatively early age so that the *rate* of growth for ages 6–8 onwards is lower than that of the Southwest Grand Bank.

The Northeast (No. 7) and East (No. 8) Grand Bank and St. Mary's Bay (No. 11) are relatively close in the 5-year-old comparisons (Fig. 10A); however, at age 15 the positions of the Northeast and East Grand Bank averages are changed in relation to that of St. Mary's Bay because of an increase in the rate of growth in the two Grand Bank areas after age 5. The two southern Grand Bank populations (No. 9 and 10) apparently grow at a more rapid rate than those to the north, except Flemish Cap, at least up to age 15.

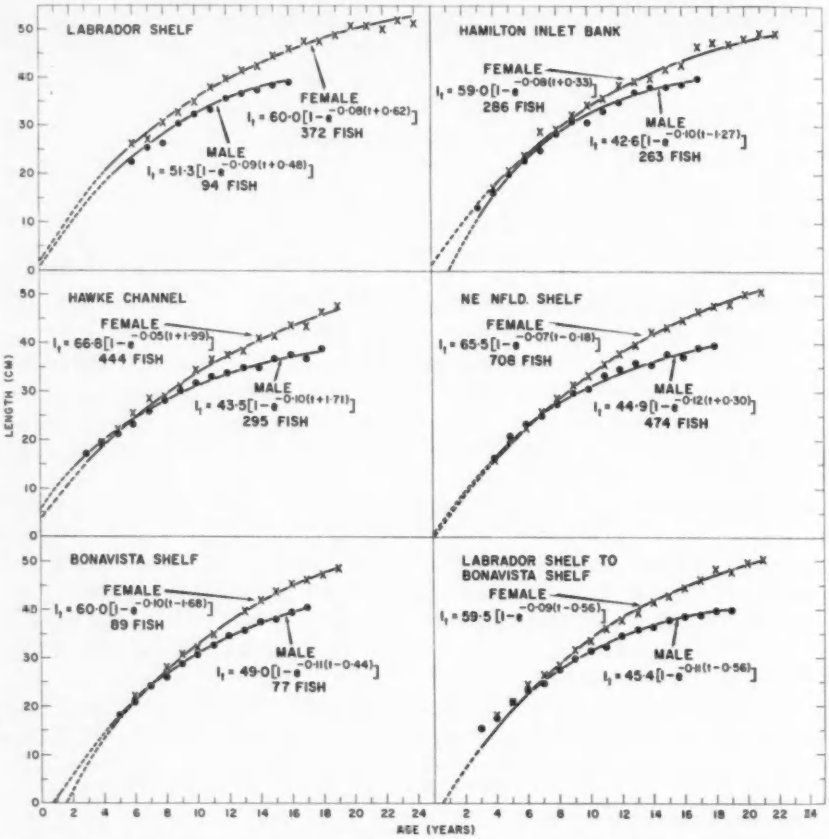

FIG. 5. Growth curves of American plaice in areas from Labrador Shelf to Bonavista Shelf.

SEASONAL GROWTH OF IMMATURE FISH FROM ST. MARY'S BAY

The average lengths of plaice of the 1952 year-class calculated from samples taken in 1957, 1958, and 1959 were used to demonstrate seasonal growth pattern (Fig. 11B). These specimens were in their 5th, 6th, and 7th years.

During 1957 the fastest growth occurred from April to August after which very little additional growth was recorded. In 1958, however, growth apparently continued until at least November. The average growth increment from April to November for the 1957 samples was about 1.9 cm, and for the 1958 samples it was 2.6 cm, nearly 1 cm more.

The growth for the April–August period was approximately the same for both 1957 and 1958; the 1957 samples indicated an increase in length from

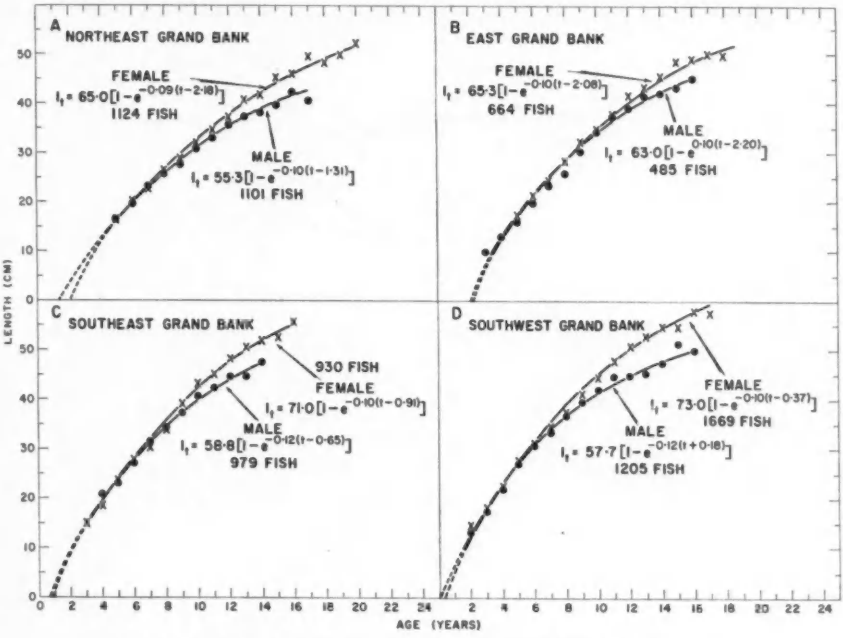

FIG. 6. Growth of American plaice for the four Grand Bank areas.

17.5 cm to 19.2 cm and the 1958 samples indicated an increase in growth from 19.9 to 21.4 cm, even though bottom temperatures in this period ranged from −1.3 to −0.4 C in 1957 compared with 0.7 to 1.5 C in 1958 (Fig. 11). The larger total growth in 1958 was apparently the result of the longer growing period in that year compared with 1957. Some growth apparently occurred during the winter of 1957–58 but little during a similar period for 1958–59.

GROWTH CURVES OF DIFFERENT YEAR-CLASSES IN ST. MARY'S BAY

The growth curves of the 1950 and 1952 year-classes for samples taken 1957 to 1963 (excluding 1962) from St. Mary's Bay (Fig. 12) were used for this comparison. These were the only groups present in sufficient numbers for the calculation of a reliable average length at a given age. Only the April–June samples were included so that the "rapid growth" period had just started. Since the difference between the average size of the male and that of the female was not great up to age 11 (Fig. 8C), the sexes were combined to increase the number of specimens. At least 50 fish were used to calculate each point on the curves.

Fish of the 1950 year-class were larger at comparable ages than those of the 1952 year-class (Fig. 12). The comparatively small growth increment of

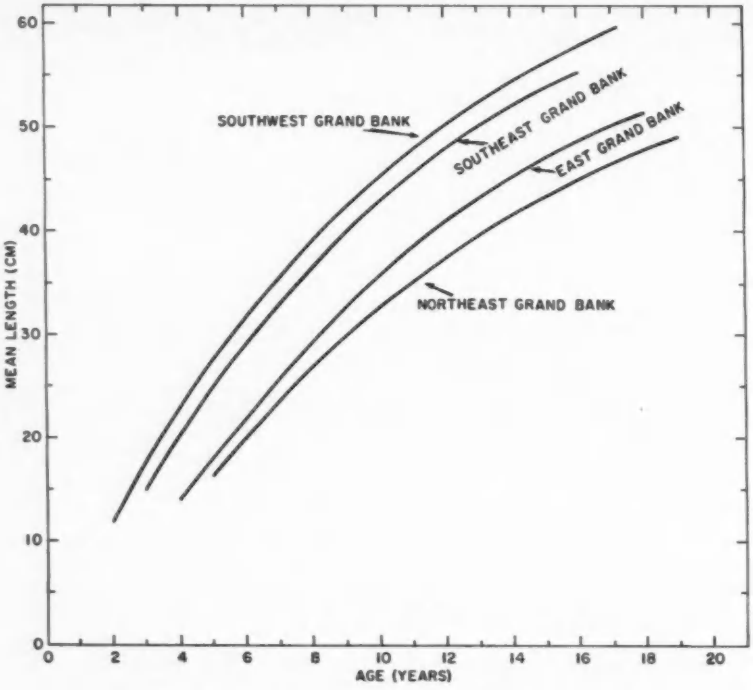

FIG. 7. Comparison of growth curves of female American plaice for four Grand Bank areas.

the 1952 year-class between the ages of 5 and 6 (growth during 1957) as indicated in a previous section (also Fig. 11) apparently accounted for the lower average length-at-age of this year-class. The average increment in 1957 (for the 1952 year-class) was about 1.9 cm, whereas for the next few years it was greater than 2.5 cm. This could have been the result of the low temperatures in that year; however, the 1950 year-class was apparently not similarly affected by adverse conditions in its early years. It is possible that, because they were 6 to 8 cm larger, they were not as drastically affected by the adverse temperatures.

YEAR-CLASS DISTRIBUTION

The range of year-classes in the populations was slightly greater for the females than for the males. The St. Mary's Bay population (Fig. 13) illustrated this; very few males survived beyond age 20, but females up to age 30 were recorded.

In Fig. 13, four year-classes can be followed from the samples for 1957–63: the 1952 and to a lesser extent the 1950, 1948, and 1946 year-classes dominated this population during the period considered here.

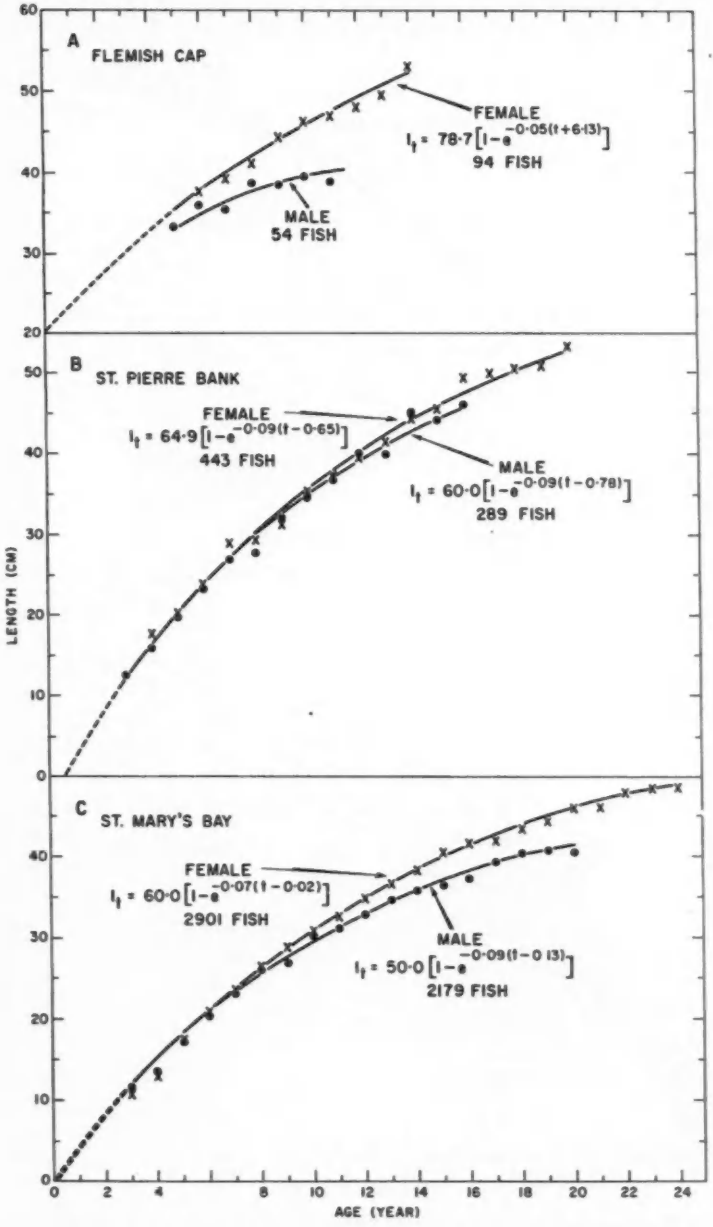

FIG. 8. Growth curves of American plaice for (A) Flemish Cap, (B) St. Pierre Bank and (C) St. Mary's Bay.

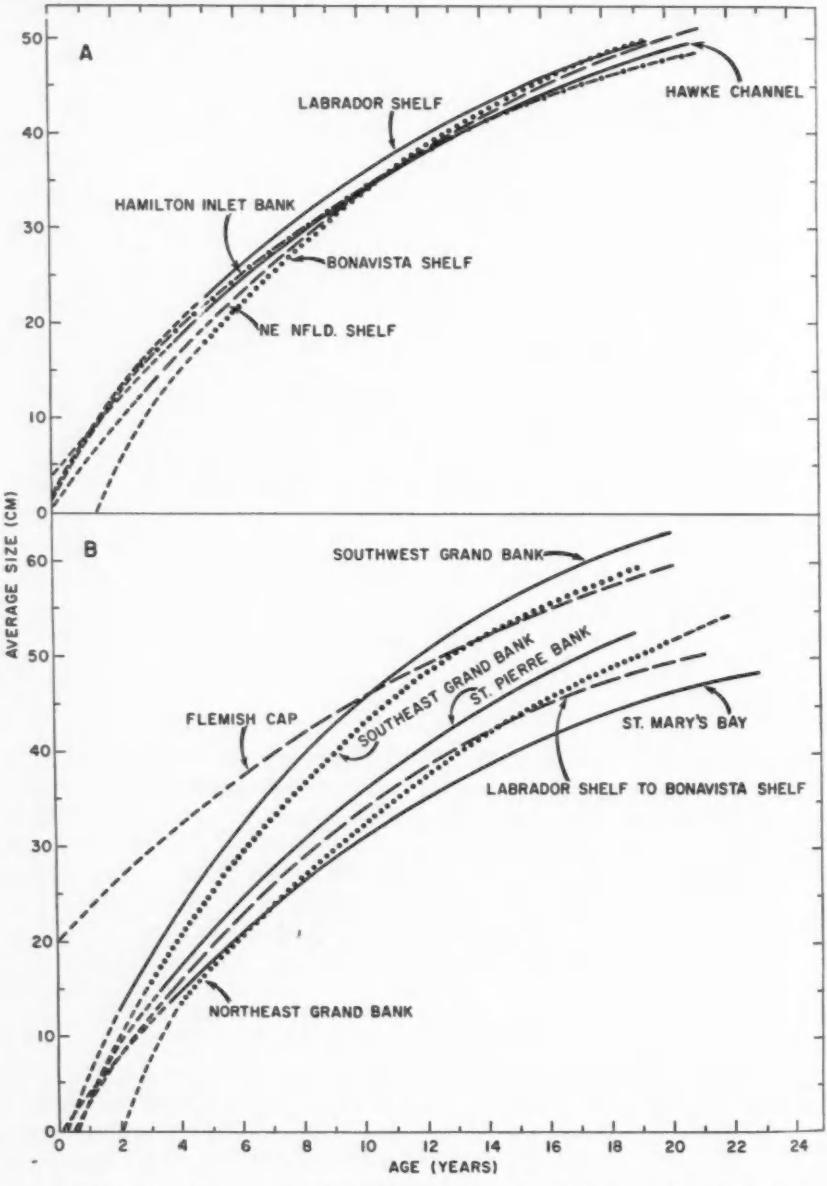

FIG. 9. Growth curve comparisons of female American plaice for various localities.

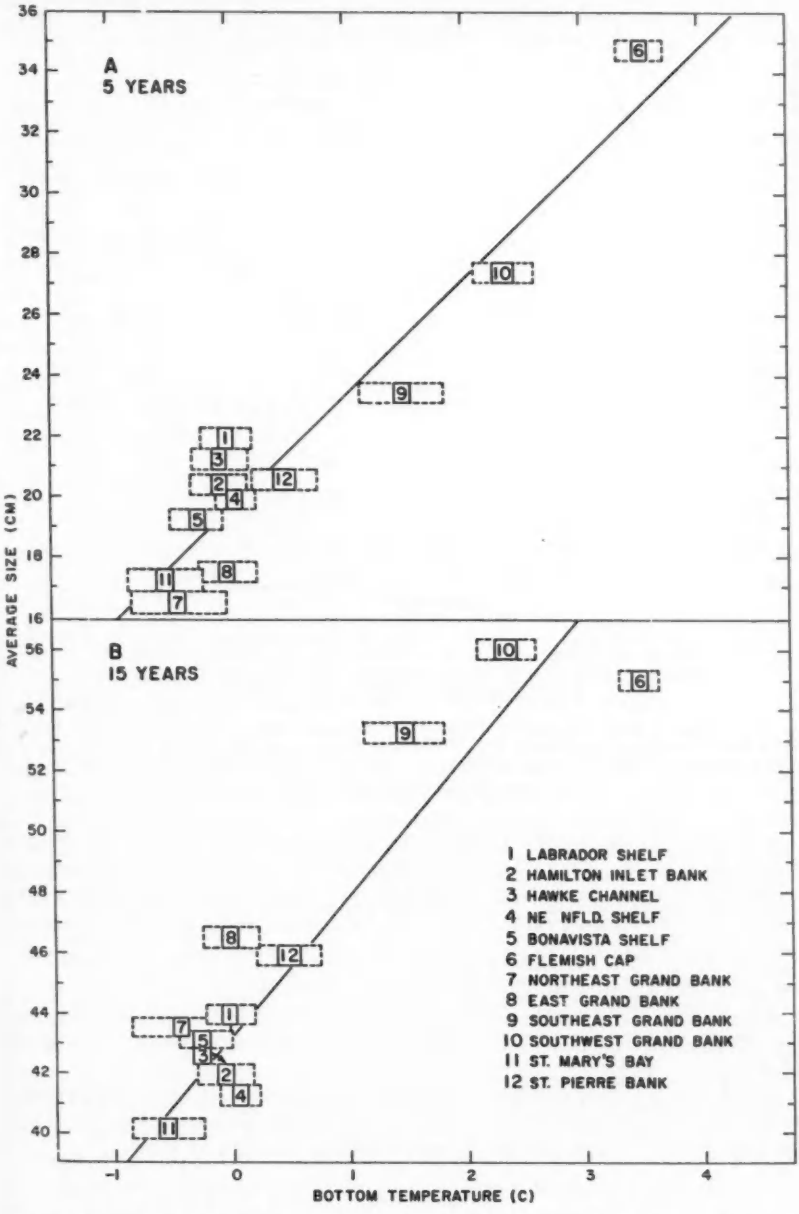

FIG. 10. Lengths at (A) age 5 and (B) age 15 of female American plaice from various areas in relation to the average bottom temperatures (solid rectangles) and probable temperature ranges (broken rectangles).

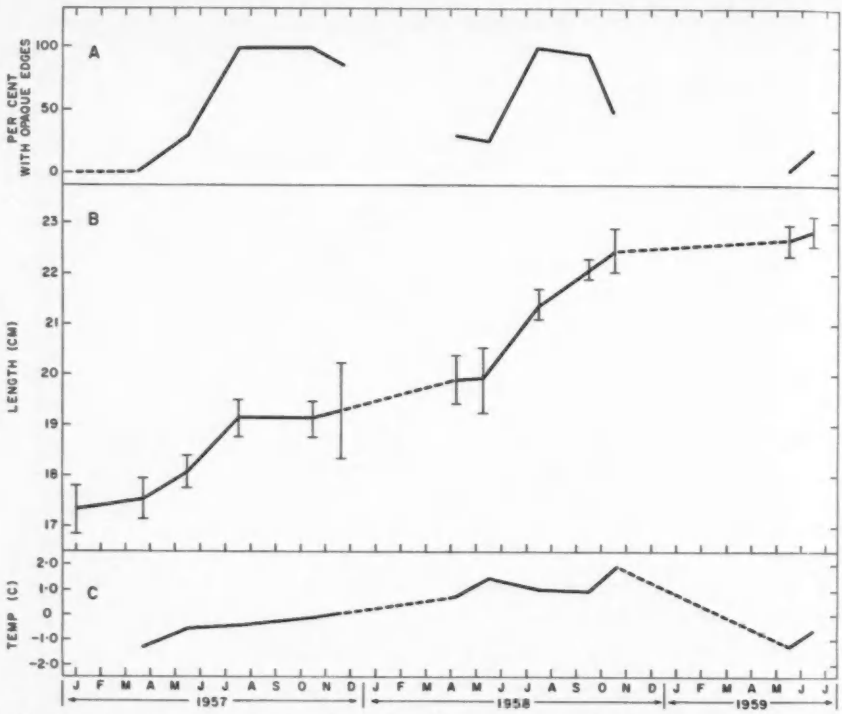

FIG. 11. A, percentages of pairs of otoliths with opaque edges in American plaice from St. Mary's Bay for indicated periods in 1957, 1958, and 1959. B, average sizes of the 1952 year-class plus and minus two standard errors for the same periods as in A. C, average bottom temperatures for the periods concerned.

The pattern of year-class distribution for the Grand Bank (Fig. 14) was different than in St. Mary's Bay and the other three areas of the Grand Bank. Several strong year-classes were recognized but were rapidly reduced in relative strength possibly by emigration or by the commercial fishery on the Southwest Grand Bank. These fish grow more rapidly than those from St. Mary's Bay and are vulnerable to the commercial otter trawl at age 3 or 4 (18–25 cm).

The other areas of the Grand Bank bore little resemblance to each other with respect to year-class survival and no year-class appeared to be dominant (Fig. 14).

The Labrador Shelf to Bonavista Shelf populations, as for all of the other populations, were composed of a large number of year-classes (Fig. 15). There is no commercial fishery for this species north of the Grand Bank.

DISCUSSION

GROWTH

Yanulov (1962) gave growth curves for some of the areas presented here. His curves for Labrador Shelf (ICNAF 2H), Northeast Grand Bank (ICNAF

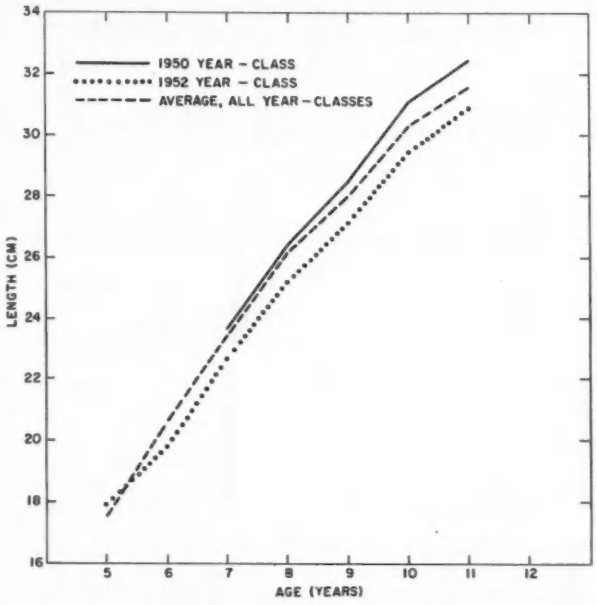

FIG. 12. Comparison of the growth of the 1950 and 1952 year-classes of American plaice from St. Mary's Bay with that of the average growth for all year-classes from that locality (samples collected from 1957 to 1961 and in 1963).

3L), and Flemish Cap (ICNAF 3M) are similar to those given here, but his curve for Hamilton Inlet Bank–Hawke Channel (ICNAF 2J) is quite different with most of his averages for length-at-age, 6–8 cm greater than those shown here. The reason for this difference is not apparent. It is possible that a different mesh size was used so that only the faster growing fish of the population were caught. However, why such a large difference should occur in one area only is difficult to understand.

Growth of fish depends ultimately on the availability and utilization of food with growth occurring when more food is obtained and digested than is required for maintenance (Brown, 1957). Maximum and minimum critical temperatures apparently control the utilization of food by the fish so that outside these limits no growth occurs regardless of the food supply. McKenzie (1934 and 1935) and Kohler (1964) suggested that, for cod, temperature was related to growth indirectly inasmuch as it controls the food consumption.

Other environmental factors may have some influence on the growth of fish but only temperature and the availability of food have been investigated to any great extent.

In relating the environment to growth there is always the possibility that fish frequently change their habitat since, as previously mentioned, plaice on

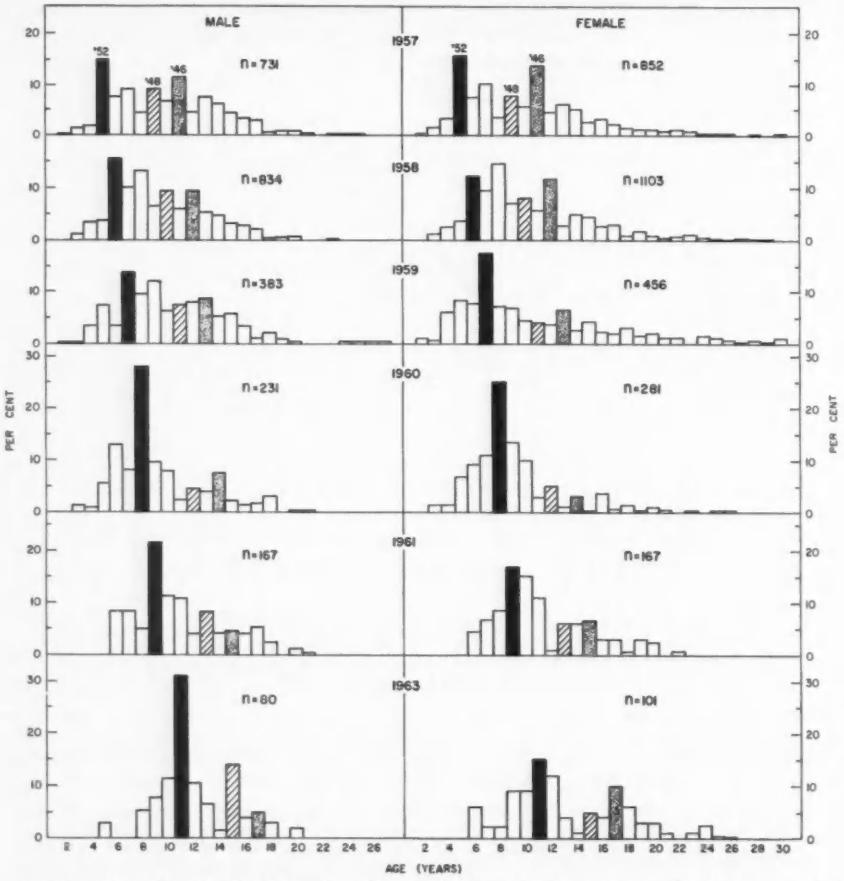

FIG. 13. Year-class distributions of American plaice from St. Mary's Bay, 1957–63. (n = number of otoliths read.)

the eastern slope of the Grand Bank apparently make seasonal migrations between deep and shallow water. This possibly changes their environmental temperature from −0.5 to 2 C.

A positive association was found, however, between the lengths at ages 5 and 10 years and the average bottom temperature for each area (Fig. 10).

Fleming (1960) showed an increase in the elevation of the growth curves of cod from the Newfoundland area from north to south. For American plaice from this area the trend is somewhat similar except for the St. Mary's Bay population (Fig. 9B). The low rate of growth here can probably be attributed to the fact that this isolated stock is always exposed to low water temperatures and also probably has a limited food supply

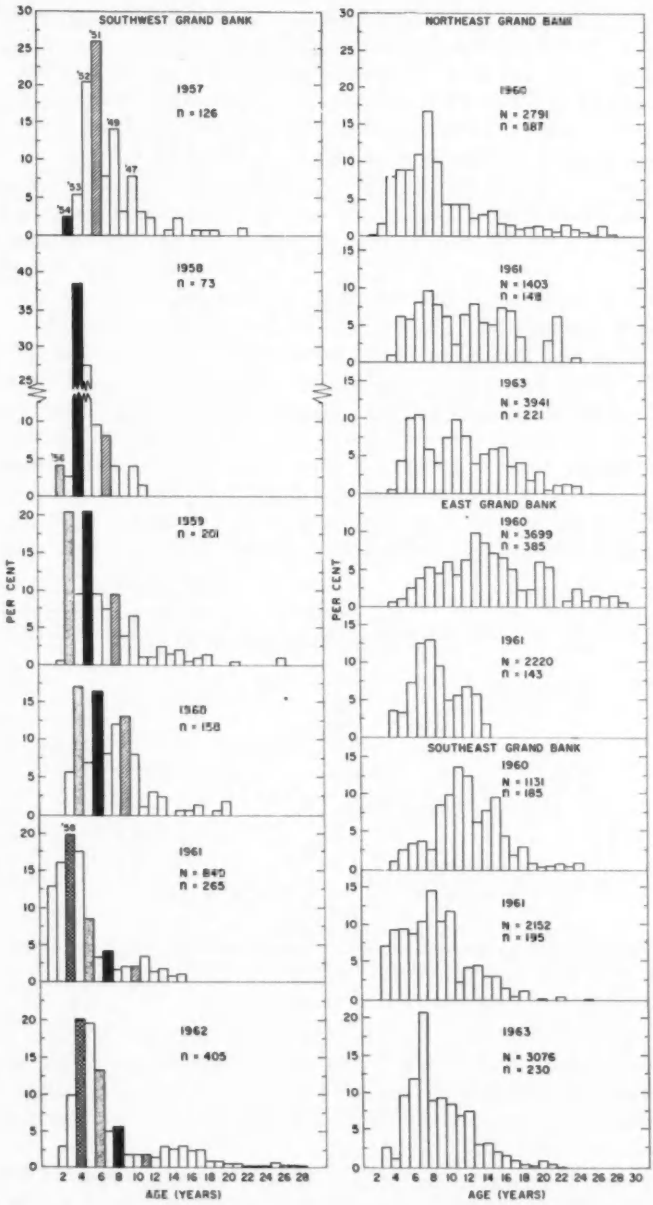

FIG. 14. Year-class distributions of female American plaice from various areas of the Grand Bank. (N is the number of fish measured and n the number of otoliths read.)

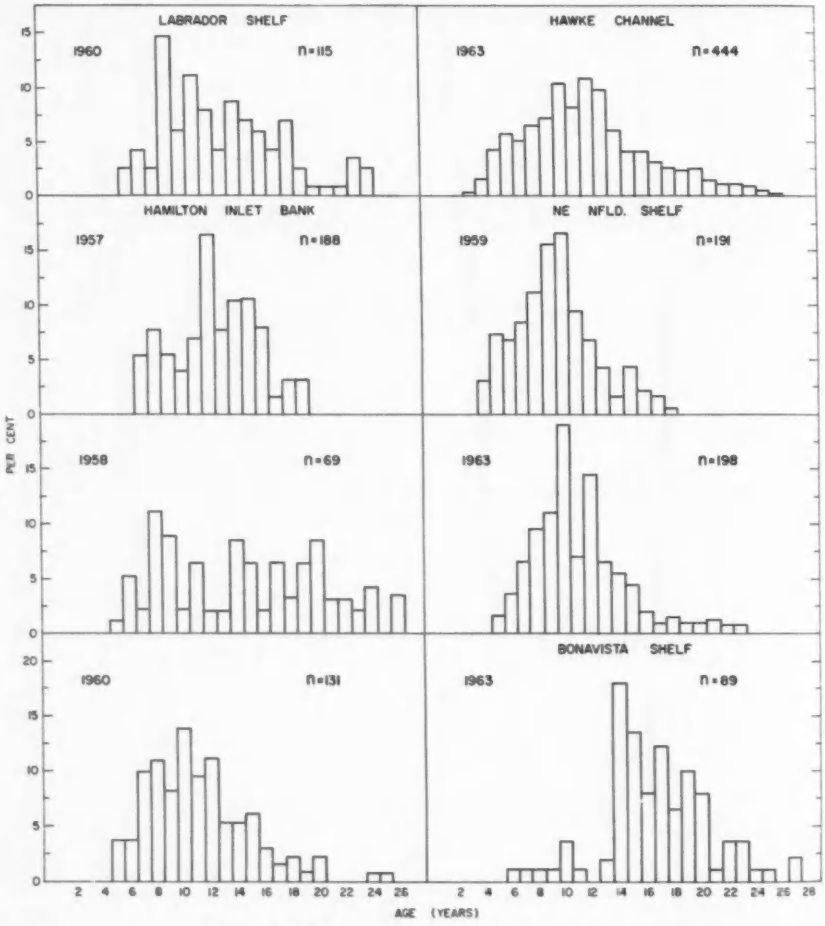

FIG. 15. Year-class distrubutions of female American plaice from the Labrador Shelf to Bonavista Shelf. (n = number in sample.)

Yanulov (1962) attributes the initial slow growth of plaice from the Northeast Grand Bank (ICNAF 3L) to the high abundance of the population and the inadequacy of the food supply for the young fish. He points out that as they grow larger they can utilize the bottom organisms such as *Echinarachnius parma*.

The Flemish Cap and Southwest Grand Bank populations are among the fastest growing fish of the whole geographic range of this species and St. Mary's Bay the slowest. Powles (1965) compares the age–length relationships of this species from several areas. Other localities have been included here to fill in

most of the geographic range of this species (Fig. 16). Female plaice only were used in the comparison. The Clyde population of the European form of *Hippoglossoides platessoides* has the shortest life span. These fish apparently live at relatively high temperatures and consequently mature early, at about age 3 (Bagenal, 1957), with a correspondingly early reduction in the growth rate.

More information on feeding and also more detailed temperature data are necessary for a better understanding of the growth pattern of this species. Growth during the first year or two appears to be important in establishing the average length-at-age for the entire life-span. Therefore, collections of 0-age and 1-year fish would be useful.

Seasonal growth. — In feeding experiments under controlled conditions with plaice, *Pleuronectes platessa*, Dawes (1930 and 1931)reported that growth ceased abruptly in November when water temperatures fell below 1 C. Growth started again just as abruptly in early March, nearly a month before this temperature was again reached. Powles (1965) stated that American plaice in the Magdalen Shallows of the Gulf of St. Lawrence drastically reduce their feeding during January–February, and Wimpenny (1949) stated that the European plaice feed most heavily from March to October.

For the Newfoundland area of the Northwest Atlantic no complete and detailed data on the seasonal feeding habits of this species were available, but

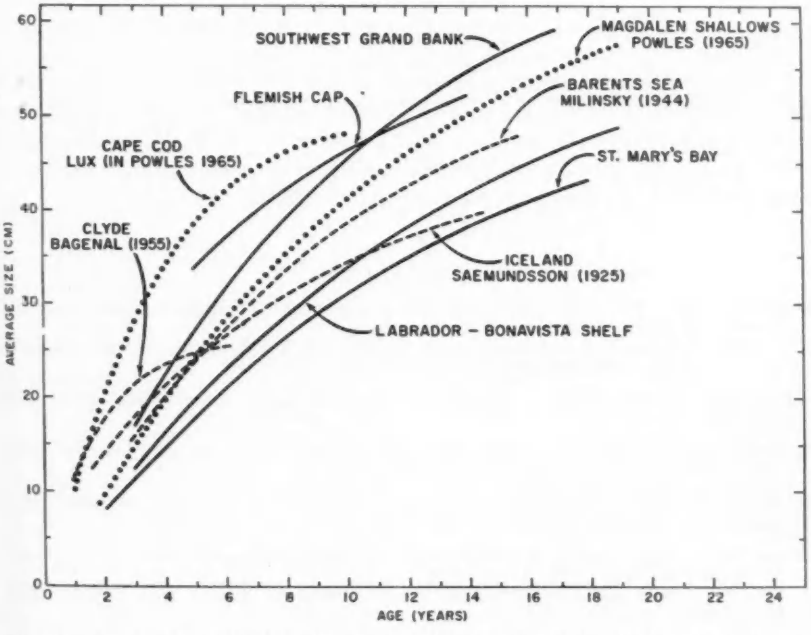

FIG. 16. Age–length relationships for female *Hippoglossoides platessoides* for different areas of its geographic distribution.

observations during routine sampling in St. Mary's Bay suggested that very little feeding occurred from December to March. Also the growth of the 1952 year-class in St. Mary's Bay in 1957–59 (Fig. 11) indicated that little growth occurred during the winter period. In 1957 new growth apparently began in May in spite of the low bottom temperatures, which did not rise above 0 C. The growth period was apparently longer in a relatively warm year (1958).

Year-Class Distribution

Year-class dominance apparently existed for the St. Mary's Bay and Southwest Grand Bank populations but for the other areas several moderately strong year-classes predominated in any particular area at any one time. Yanulov's (1962) age-frequencies gave a similar picture for the various areas that he presented.

Although for any particular area and year plaice of a wide age-range were found, there is evidence from research surveys that large quantities of baby plaice (3–5 years) live principally on the shallow parts of the Grand Bank (40 fath, 73 m) and at 100 fath (183 m) on the continental shelf to the north of the Grand Bank (unpublished data, Biological Station, St. John's Nfld.). It therefore seems probable that these localities act as nursery areas for the large commercial population located along the seaward slope of the Grand Bank.

ACKNOWLEDGMENTS

The author is particularly indebted to Mr C. A. Rose who did most of the calculations involved and with the author made all of the age determinations. Grateful acknowledgment is also extended to Mr E. J. Sandeman and Mr V. M. Hodder for many helpful suggestions in the preparation of the manuscript and Mr E. L. Rowe for photographs of otoliths.

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Fatty Acid Composition of Some Marine Animals from Various Depths[1,2]

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ABSTRACT

The fatty acid composition of 20 species of marine animals, primarily fishes and crustaceans, was determined by gas–liquid chromatography. The species came from various depths down to 4400 m. The results showed that the medium-chain saturated and the long-chain polyunsaturated acids decreased with increasing depth, while oleic acid increased. It was thought that this indicated the presence of large amounts of wax esters. A benthic, mud-feeding holothurian *Scotoplanes theeli* was shown to have a fatty acid composition markedly different from that of pelagic species. This was attributed in part to the bacterial components of its diet.

INTRODUCTION

Until recently, studies of deep-sea organisms have centered largely on their taxonomy and distribution, with very little attention given to their biochemistry. However, the fatty acid composition of some deeper pelagic animals has been observed (Lewis, 1962) to differ from that of animals living at the surface in having greater relative amounts of oleic acid. The present survey was undertaken to determine the extent of this difference, the consistency with which it is demonstrated in deep-sea animals, and its correlation with depth of habitat.

Recently some deeper pelagic fish have been reported (Nevenzel et al., 1965, 1966) to have large amounts of wax esters which are characterized by a predominance of oleic acid. These authors suggest that the wax esters may serve to achieve neutral buoyancy. A general survey of fatty acid composition of deep-dwelling organisms may offer evidence on this question.

MATERIALS

The organisms used in this study were typical components of trawls taken at various times during 1964 and 1965 in the deeper waters off San Diego and Baja California. Representative surface material included in the analysis for comparison was collected in local, inshore waters. A typical mud-feeding benthic species, the holothurian *Scotoplanes theeli*, was obtained from an Isaacs-Kidd trawl which dredged in the Cedros Trench off Baja California at a depth of about 4400 m.

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[2]This work, supported in part by the Institute of Marine Resources, forms part of a thesis submitted to the University of California, San Diego, in partial fulfilment of the requirements for thed egree of Doctor of Philosophy. The Institute of Artic Biology (NIH Grant #GM-10402) assisted in the preparation of the manuscript.
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The specimens ranged in length from 3 or 4 to 30 or more cm. A distinction between depot, liver, and muscle lipids was not feasible in the smaller organisms and was not attempted in the larger. When size precluded total extraction, a section of muscle and skin was analyzed. Four species, all fishes, were analyzed in this manner: the hagfish, *Eptatretus deani*, the snipe eels, *Serrivomer sector* and *Avocettina bowersi*, and the rattail, *Coryphaenoides acrolepis*.

The specimens were all of apparent maturity except for the Pacific saury, *Cololabis saira*, which were dipnetted at the surface and averaged 4 cm in length. Since adults of this species are 30 cm or more in length, these were obviously very immature.

The oceanic environment has been subdivided according to several schemes; in this study the system of Hedgpeth (1957) is adopted: epipelagic designates the zone from the surface to 150 m, mesopelagic that from 150 to 1000 m, and bathypelagic that from 1000 to 4000 m. Benthic (bottom-living) designations are as follows: sublittoral to depths of 300 m, mesobenthic to 1000 m, bathybenthic to 4000 m, and abyssobenthic at greater depths. The designation of a particular zone as the normal habitat of an organism was based on the judgment of specialists in the several groups. Such designations must be regarded as only generally valid. Precise localization of the pelagic organisms was not possible with the nonclosing Isaacs-Kidd trawls used for collections, nor was it feasible, since many of the pelagic organisms execute extensive diurnal migrations.

A list and classification of the species utilized follows (see also Table I).

CRUSTACEA
Lophogastridae, Order Mysidacea
1. *Gnathophausia gracilis* (Willemoes-Suhn). Bathypelagic.
Oplophoridae, Order Decapoda
2, 3. *Acanthephyra curtirostris* (Wood-Mason). Bathypelagic.
Pasiphaeidae, Order Decapoda.
4. *Pasiphaea* sp. Bathypelagic.
Galatheidae, Order Decapoda
5. *Pleuroncodes planipes*. (Stimson): Benthic, sublittoral.

ECHINODERMATA
Class Holothuroidea.
6. *Scotoplanes theeli* (Ohshima): Abyssobenthic.

PISCES
Myxinidea — hagfishes
7. *Eptatretus deani* (Evermann and Goldsborough): Bathybenthic.
Engraulididae — anchovies
8. *Engraulis mordax mordax* (Girard): Epipelagic to upper mesopelagic.
Alepocephalidae — slickheads
9. *Bajacalifornia burragei* (Townsend and Nichols): Bathypelagic.
Argentinidae — deepsea smelts
10. *Leuroglossus stilbus* (Gilbert): Epilagic to mesopelagic.
Sternoptychidae — lightfishes
11. *Vinciguerria lucetia* (Garman): Epipelagic to mesopelagic.

12. *Argyropelecus lychnus* (Garman): Mesopelagic.
Scomberesocidae — sauries
13. *Cololabis saira* (Brevoort): Epipelagic.
Myctophidae — lanternfishes
14. *Scopelengys tristis* (Garman): Bathypelagic.
15. *Myctophum nitidulum* (Garman): Mesopelagic.
16. *Triphoturus mexicanus* (Gilbert): Upper Bathypelagic.
Nemichthyidae — snipe eels
17. *Serrivomer sector* (Garman): Bathypelagic.
18. *Avocettina bowersi* (Garman): Bathypelagic.
Coryphaenoididae — rattails
19. *Coryphaenoides* cf. *acrolepis* (Bean): Mesobenthic.
Cynoglossidae — tongue soles
20. *Symphurus atricauda* (Jordan and Gilbert): Benthic, sublittoral.

METHODS

The material collected for this study was promptly frozen and stored at −26 C. For analysis, the specimens were thawed, blotted dry, and homogenized in a Waring Blendor in approximately 10-fold their volume of chloroform–methanol 2:1 (v/v). The homogenate was held at room temperature for several hours before being filtered. The filtrate was washed with 0.2 vol of NaCl solution of 73% saturation and then evaporated to near-dryness under N_2 in a 60 C water bath or under reduced pressure in a rotary evaporator, depending upon volume.

Saponification followed standard procedures: the washed extract was refluxed in 1.4 N KOH in 95% ethanol for 1 hr, an equivalent volume of water was added, and the nonsaponifiable fraction was extracted twice with hexane and once with 1:1 (v/v) solution of hexane and diethyl ether. The aqueous layer was then acidified with 10% H_2SO_4 and the fatty acids were extracted into hexane. They were methylated by refluxing for 1 hr in a solution of 1% H_2SO_4 in methanol, followed by the addition of an equal volume of water and extraction of the methyl esters into hexane.

Analyses were made with a Loenco Model 70 dual column gas chromatograph equipped with thermal conductivity detectors. During the latter part of this study, flame ionization detectors were installed. Two columns were used: (1) a $\frac{1}{4}$-inch × 2-ft stainless steel column containing 20% SE-30, a methyl-substituted silicone rubber (General Electric Co.) on 60–80-mesh Chromosorb W, acid washed, and hexamethyldisilazane-treated, and (2) a $\frac{1}{4}$-inch × 4-ft copper column containing 20% diethylene glycol succinate (hereafter referred to as DEGS) on 60–80-mesh Chromosorb W, acid washed, and treated with dimethyldichlorosilane. The SE-30 column was operated at 220 C; the injection port was at 260 C and the detector oven at 250 C. Helium flow was 105 ml/min for both columns. The DEGS column was operated at 190 C for isothermal analyses, and from 175 to 210 C on temperature-programmed analyses having a temperature rise of 4 C degrees/min. The other conditions were the same as with the SE-30 column. Filament current was 90 ma.

A number of steps were required for each fatty acid determination. The first analysis was made with the DEGS column under isothermal conditions to obtain the major retention values. The second analysis was made on the SE-30 column; the resolution of this short column was adequate only for the separation of fatty acids into carbon number families (Fig. 1). Initially, the C-20 and C-22 acids were each collected at the detector outlet in glass U-tubes containing a small plug of glass wool (Fig. 2). The collections were then re-analyzed on DEGS for retention values which could be identified in the full spectrum. Later, the C-16 and C-18 peaks were likewise collected and analyzed (Fig. 3).[4] Finally, a temperature-programmed analysis of the total esters was made on DEGS for quantification (see Table I). The fatty acids were identified by the method of Ackman (1963) in which the logarithms of the relative retention values are plotted against carbon number.

The SE-30 analysis, necessary for the above-mentioned collections, provided additional information of value: the weight-percentage composition by carbon number serves as a useful confirmation of the DEGS analyses when the latter results are pooled into similar terms. The two sets of values for 9 of the 20 analyses in this study are seen (Table II) to be in reasonable agreement, generally within the 2–3% replication error.

Peak areas were obtained by the use of a Disc Integrator, except as noted below, and were corrected for nonlinearity of detector response by the method recommended by Horning et al. (1964) in which the area is multiplied by the square-root of the molecular weight. The corrected area divided by the total corrected area then gave the weight per cent composition. Four analyses

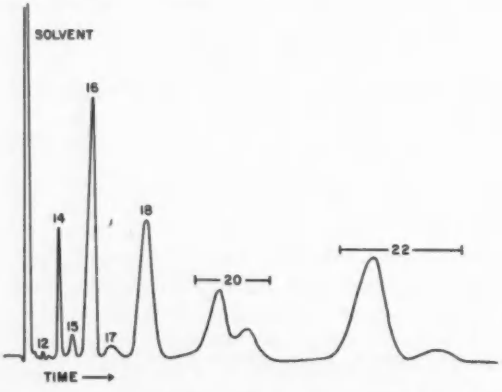

FIG. 1. Gas chromatographic analysis of the fatty acid methyl esters from *Myctophum nitidulum* on the SE-30 column, showing fatty acid carbon families.

[4]During preparation of this manuscript, Smith and White (1966) reported the use of a similar technique to separate a synthetic mixture of fatty acid methyl esters into chain length fractions.

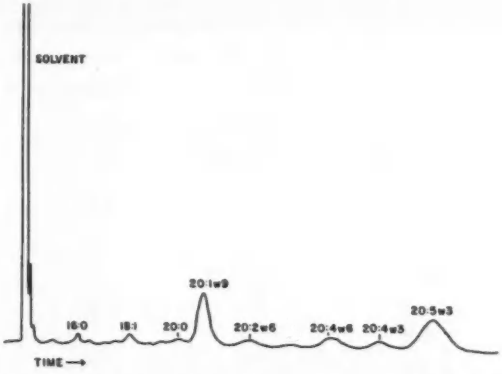

FIG. 2. Gas chromatographic analysis of the C-20 fatty acid methyl esters from *Myctophum nitidulum*, collected from an SE-30 column and reanalyzed on a DEGS column. (Designations are: carbon number, number of double bonds, and end carbon chain.)

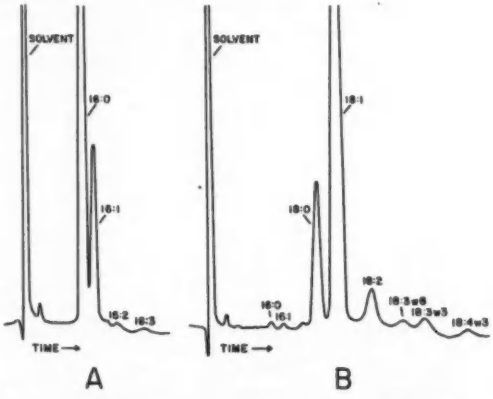

FIG. 3. Gas chromatographic analysis of fatty acid methyl esters from *Myctophum nitidulum* collected from an SE-30 column and reanalyzed on a DEGS column. A, C-16 fatty acids; B, C-18 fatty acids.

were made without the aid of the Disc Integrator; the peak areas were calculated by triangulation and corrected as mentioned above. In the few cases where flame ionization was employed, the uncorrected peak areas gave the weight per cent directly.

A report of serious losses of polyunsaturated acids on polyester columns (Gerson et al., 1966) which appeared during preparation of this manuscript called for tests to determine whether similar losses had occurred in this study. The columns and instrument from which this data had been obtained were

TABLE I. Fatty acid composition in weight per cent (w/w) as determined by GLC. The results are arranged according to depth of habitat, shallow to deep, left to right.

Genus:	*Cololabis* (immature)	*Symphurus*	*Pleuroncodes*	*Engraulis*
Habitat:	Epipelagic	Benthic, sublittoral	Benthic and epipelagic	Epipelagic
Fatty acid				
14:0	3.4	1.1	4.7	7.7
15:0	0.8	0.8	2.0	1.0
16:0	30.4	20.2	22.7	21.6
16:1ω7	6.3	4.6	8.4	10.9
16:2ω4	1.0	1.8	1.3	tr
16:3ω4	0.7	1.0	tr	1.0
17's[a]	2.3	5.4	3.7	0.7
18:0	9.7	9.6	4.7	4.8
18:1ω9	13.5	14.1	17.3	18.5
18:2ω6	0.7	0.7	2.2	5.0
18:3ω3	tr	tr	tr	tr
20:0	–	–	–	tr
20:1ω9[b]	1.7	2.6	1.7	1.6
20:2ω6	1.0	tr	1.3	4.5
20:3ω6	tr	tr	tr	tr
20:4ω6	2.1	5.0	3.0	0.4
20:4ω3	0.2	tr	tr	tr
20:5ω3	5.5	8.8	16.8	13.5
22:1ω9	–	2.0	–	–
22:3ω6	–	2.2	–	–
22:4ω6	tr	0.7	tr	–
22:4ω3	tr	–	–	–
22:5ω6	–	–	–	–
22:5ω3	0.6	2.6	tr	0.6
22:6ω3	22.2	22.1	13.9	8.8

	Vinciguerria	*Leuroglossus*	*Myctophum*	*Argyropelecus*
	Epipelagic mesopelagic	Epipelagic mesopelagic	Mesopelagic	Mesopelagic
14:0	5.4	4.6	3.5	3.5
15:0	1.3	1.4	0.5	1.1
16:0	26.5	25.5	27.0	22.0
16:1ω7	3.5	4.7	7.2	6.4
16:2ω4	1.2	tr	tr	0.6
16:3ω4	tr	–	0.6	0.6
17's[a]	tr	2.1	1.2	3.8
18:0	6.0	6.3	4.2	6.1
18:1ω9	15.4	25.4	26.9	31.6
18:2ω6	1.5	5.7	0.9	1.4
18:3ω3	tr	–	0.3	tr
20:0	–	0.2	0.2	–

(*Continued*)

TABLE I. Fatty acid composition in weight per cent (w/w) as determined by GLC. The results are arranged according to depth of habitat, shallow to deep, left to right. (*Continued*)

	Vinciguerria Epilagic mesopelagic	*Leuroglossus* Epilagic mesopelagic	*Myctophum* Mesopelagic	*Argyropelecus* Mesopalegic
20:1ω9[b]	1.1	14.7	2.7	4.5
20:2ω6	1.7	0.7	0.7	0.7
20:3ω6	tr	1.1	tr	tr
20:4ω6	1.3	–	0.7	2.6
20:4ω3	tr	0.5	0.4	0.3
20:5ω3	7.0	2.8	4.1	3.8
22:1ω9	–	3.3	0.6	–
22:3ω6	–	1.1	–	0.6
22:4ω6	1.9	–	0.6	–
22:4ω3	1.2	tr	tr	0.4
22:5ω6	–	–	–	–
22:5ω3	tr	0.5	0.6	0.4
22:6ω3	26.5	6.4	12.5	13.5

	Coryphaenoides Mesobenthic (muscle and skin)	*Bajacalifornia* Bathypelagic	*Scopelengys* Bathypelagic	*Serrivomer* Bathypelagic (muscle and skin)
14:0	1.3	1.4	2.8	1.6
15:0	0.8	0.6	0.7	0.4
16:0	17.0	17.2	19.1	26.2
16:1ω7	6.8	11.0	6.9	5.8
16:2ω4	1.0	1.6	tr	tr
16:3ω4	2.1	1.2	1.2	1.9
17's[a]	tr	3.4	2.9	2.2
18:0	3.0	3.7	3.7	4.1
18:1ω9	30.2	31.4	33.0	38.3
18:2ω6	2.0	0.2	0.7	1.3
18:3ω3	tr	tr	tr	tr
20:0	–	–	–	–
20:1ω9[b]	5.6	4.8	6.5	3.8
20:2ω6	0.6	tr	0,5	0.9
20:3ω6	tr	–	–	–
20:4ω6	5.0	2.5	1.8	3.8
20:4ω3	0.3	tr	–	tr
20:5ω3	3.0	3.6	2.8	3.2
22:1ω9	–	2.5	4.1	–
22:3ω6	–	–	–	–
22:4ω6	0.8	2.5	1.8	–
22:4ω3	0.7	0.2	–	–
22:5ω6	–	–	1.0	–
22:5ω3	0.8	0.3	0.5	–
22:6ω3	19.0	15.0	12.8	8.7

(*Continued*)

TABLE I. Fatty acid composition in weight per cent (w/w) as determined by GLC. The results are arranged according to depth of habitat, shallow to deep, left to right. (*Continued*)

	Eptatretus Bathybenthic (muscle and skin)	*Triphoturus* Bathypelagic	*Pasiphaea* Bathypelagic	*Avocettina* Bathypelagic (muscle and skin)
14:0	3.4	0.2	2.3	1.2
15:0	0.5	tr	0.6	tr
16:0	16.2	2.9	11.9	16.0
16:1ω7	8.5	5.5	9.4	6.7
16:2ω4	0.7	–	tr	tr
16:3ω4	0.7	6.4	0.6	2.0
17's[a]	1.5	1.0	2.7	1.0
18:0	3.3	–	1.0	3.0
18:1ω9	53.0	70.6	38.6	42.6
18:2ω6	0.7	1.1	1.2	1.2
18:3ω3	0.1	–	0.3	–
20:0	–	–	–	–
20:1ω7[b]	3.2	2.2	5.3	6.0
20:2ω5	0.3	0.4	1.1	tr
20:3ω6	–	–	–	–
20:4ω5	1.8	1.1	0.7	3.3
20:4ω3	–	tr	tr	tr
20:5ω3	0.4	3.6	6.8	4.6
22:1ω9	–	–	7.7	2.0
22:3ω6	–	–	–	–
22:4ω6	0.4	tr	4.0	tr
22:4ω3	–	tr	–	–
22:5ω6	–	–	–	tr
22:5ω3	5.8	tr	–	tr
22:6ω3	0.9	6.0	8.5	13.4

	Gnathophausia Bathypelagic	*Acanthephyra* No. 1 Bathypelagic	*Acanthephyra* No. 2 Bathypelagic
14:0	0.8	0.2	0.3
15:0	0.3	0.3	tr
16:0	6.3	2.5	1.7
16:1ω7	11.5	9.9	6.4
16:2ω4	tr	–	0.8
16:3ω4	3.7	0.3	–
17's[a]	1.3	1.5	0.4
18:0	tr	–	–
18:1ω9	50.6	71.7	76.9
18:2ω6	1.6	1.1	1.1
18:3ω3	–	–	–
20:0	–	–	–
20:1ω9[b]	7.5	2.9	5.3

(*Continued*)

TABLE I. Fatty acid composition in weight per cent (w/w) as determined by GLC. The results are arranged according to depth of habitat, shallow to deep, left to right.— (*Concluded*)

	Gnathophausia Bathypelagic	*Acanthephyra* No. 1 Bathypelagic	*Acanthephyra* No. 2 Bathypelagic
20:2ω6	0.5	0.2	0.3
20:3ω6	–	–	tr
20:4ω6	4.8	0.6	1.1
20:4ω3	–	tr	0.3
20:5ω3	5.9	1.9	0.7
22:1ω9	–	1.2	–
22:3ω6	–	–	–
22:4ω6	–	tr	0.4
22:4ω3	tr	0.3	0.2
22:5ω6	–	–	–
22:5ω3	–	–	tr
22:6ω3	6.3	6.3	4.4

[a]Determined on SE-30.
[b]Includes 18:4ω3.

not available but the tests were conducted with virtually identical conditions and components. The SE-30 column differed only in having pretreatment with dimethyldichlorosilane rather than hexamethyldisilazane; the DEGS column was 1 ft longer than the original. The test mixture was made up of 36.50 mg of methyl stearate, which undergoes no loss and serves as reference standard, and 21.00 mg of methyl arachidonate of 90+% purity (Applied Science). Peak areas were calculated by triangulation and, because of flame ionization detection, were uncorrected. The SE-30 and DEGS columns were used for three analyses each and showed losses of methyl arachidonate not exceeding 2.3% and, in one instance, a gain of 1.6%, findings which are within the range of experimental error. Evidently the losses which have been reported result from some as yet unknown operating parameter and are not a necessary consequence of the use of polyester columns. In regard to the present study, it can be concluded that the corrections used for nonlinearity of the thermal conductivity detector were adequate.

To verify the overall accuracy, four replicate analyses were made of a test mixture of C-12 to C-18 fatty acid methyl esters which spanned a three-fold range in concentration and included members having one and two double bonds. The DEGS column and flame ionization were used as previously described and peak areas were obtained by triangulation. Standard deviations ranged between 1.45 for methyl myristate and 0.026 for methyl oleate.

In the course of this study, specimens from the benthos occasionally became available. Exploratory analyses were made on an unidentified gastropod and brittle star dredged from 900 m in the San Diego Trough. Both

TABLE II. Comparison of fatty acid composition in weight per cent by carbon numbers as determined on two GLC columns. For species identification see text. (Nine analyses presented from a total of twenty.)

Fatty acid carbon no.	*Cololabis* SE-30 DEGS (%)		*Symphurus* SE-30 DEGS (%)		*Pleuroncodes* SE-30 DEGS (%)	
14	2.0	3.4	1.5	1.1	4.4	4.7
15	1.4	0.8	1.7	0.8	1.4	2.0
16	31.5	38.4	23.3	27.6	26.7	32.4
17[a]	2.3		5.4		3.7	
18	28.6	24.6	21.7	24.4	26.5	24.2
20	8.9	10.5	17.3	16.4	19.9	22.8
22	22.2	22.8	29.1	29.6	17.4	13.9
	Engraulis SE-30 DEGS (%)		*Vinciguerria* SE-30 DEGS (%)		*Leuroglossus* SE-30 DEGS (%)	
14	8.3	7.7	5.3	5.4	3.7	4.6
15	1.0	1.0	1.3	1.3	0.7	1.4
16	36.0	33.5	29.3	31.2	27.3	30.2
17[a]	0.7		tr		2.1	
18	25.8	28.3	24.2	22.9	33.7	37.4
20	16.9	20.0	9.5	11.1	20.0	20.0
22	11.4	9.4	30.4	29.6	12.4	11.3
	Myctophum SE-30 DEGS (%)		*Argyropelecus* SE-30 DEGS (%)		*Coryphaenoides* SE-30 DEGS (%)	
14	3.5	3.8	2.4	3.5	0.8	0.8
15	0.5	1.1	0.8	1.1	0.6	0.5
16	33.3	34.9	25.9	29.6	24.0	30.6
17[a]	1.1		3.8		2.1	
18	35.6	32.3	40.3	39.1	28.3	26.0
20	9.0	8.6	10.1	11.9	14.8	16.0
22	16.8	14.3	16.2	14.9	28.5	26.0

[a]Determined only on SE-30.

were believed to be mud-detrital feeders. Full identification of the fatty acids was not made, but it was immediately apparent that the patterns found in the pelagic organisms were replaced in these species with more complicated spectra which did not show the high levels of oleic acid.

Later, several specimens of the holothurian *Scotoplanes theeli*, averaging 5 cm in length, were obtained from about 4400 m in the Cedros Trench off

Baja California. Their intestinal tracts were filled with mud which was rinsed out through an incision in the side. The holothurian, which at this stage resembled an empty sack, was treated to the customary extraction and saponification. Ultimately, two of these holothurians were analyzed. The first analysis was exploratory and a detailed identification of fatty acids was not obtained, but the composition by carbon number (from the SE-30 column) agreed generally with the analysis of the second specimen which was obtained by the carbon number reanalysis technique previously described, except that the odd-numbered fatty acids were included.

RESULTS AND DISCUSSION

In order to examine the analytical results for significant changes, they must be listed according to the depth of habitat of the various species. This presents no problem with the near-surface species, but the extensive diurnal migrations undertaken by organisms in the mesopelagic zone makes any classification by depth somewhat artificial. Although the organisms of the bathypelagic zone are not known to migrate diurnally, the comparative lack of knowledge calls for a degree of arbitrariness if the species must be ranked according to depth within the zone. As indicated earlier, the designations were obtained from specialists in the several groups and were based upon records showing the average depth of capture. Subject to these limitations, the fatty acid compositions are listed according to habitat (Table I) from epipelagic and sublittoral on the left to bathypelagic and bathybenthic on the right, and are summarized in graphic form in Fig. 4.

A trend can be seen toward a predominance of oleic acid with increasing depth, while the other major acids are reduced accordingly, except 16:1ω7[5] which remains nearly the same in all the species. Oleic acid levels range from about 15% of the total fatty acids in the surface species to 72 and 77% in the deepest-dwelling species, the shrimp *Acanthephyra curtirostris*. The saturated acids 16:0 and 18:0 are reduced to very low levels in most of the bathypelagic species as are the polyunsaturated C-20s and C-22s.

The relatively large amount of oleic acid found in some of the deeper fish and crustaceans is undoubtedly caused by high levels of wax esters similar to those found by Nevenzel et al. (1965, 1966) in midwater fishes. Their analysis of *Triphoturus mexicanus* revealed that 51% of the muscle lipids were wax esters and that the total carcass fatty acids contained 75% oleic acid, agreeing with the 71% found in this study (Nevenzel, personal communication). In their studies of the lipids of the coelacanth and the "castor oil" fish they found that wax esters comprised 92.7 and 91.5% of the muscle lipid respectively. These wax esters contained 71 and 77% oleic acid each. It seems probable that the high oleic acid levels found in this study reflect a similar situation, thus indicating that the deposition of wax esters may be common among the

[5]Omega designates the end carbon chain counting from the terminal methyl group.

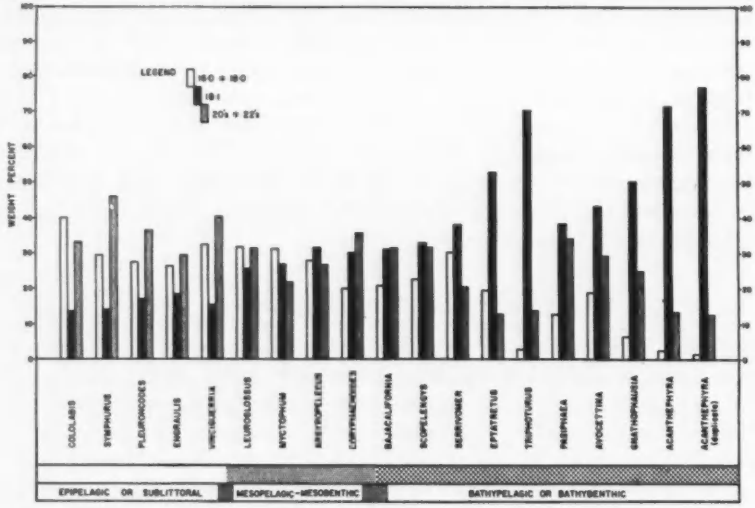

FIG. 4. Summarized fatty acid composition arranged according to depth of habitat: shallow to deep from left to right.

deeper fishes and crustaceans. This offers support to the suggestion of Nevenzel et al. (1966) that wax esters might serve to achieve neutral buoyancy.

The marked differences in fatty acid composition between the deeper pelagic species and the true benthic species (gastropod, brittle star, and holothurians) might also be regarded as supporting the buoyancy hypothesis. While diet may account for much of the difference, as will be discussed later, the lack of high levels of oleic acid in these crawling bottom-dwellers is compatible with a situation requiring no buoyancy and consequently no wax esters. The two epibenthic carnivorous fishes, the rat-tail *Coryphaenoides* and the hagfish *Eptatretus*, similarly would require no aid in buoyancy since the former is equipped with a swim bladder and the latter lives on the bottom. The elevated levels of oleic acid seen in these two may result from pelagic components in the diet.

The analysis of the holothurian is of particular interest for the depth of its habitat — 4400 m. Aside from the moderate amount of oleic acid, already discussed, the spectrum is unique for the large percentages of 20:4ω6 and 20:5ω3. The latter acid is typical of marine oils and is generally seen (Klenk and Eberhagen, 1962) in large amounts only when the other major marine polyunsaturated acid, 22:6ω3, is at a reduced level, as in the case of the holothurian. However, arachidonic acid rarely exceeds 5% in total carcass lipids of marine animals (Klenk and Eberhagen, 1962) and is regarded as characteristic of phospholipids (Olley and Duncan, 1965). Its presence in the holothurian (identification was quite firm) at 21% of the total fatty acids has no ready explanation.

Another interesting feature of the holothurian fatty acid spectrum is that the branched chain fatty acids are present in greater amounts than in the lipids of higher marine organisms as reported by Ackman and Sipos (1965). The resolution of the DEGS column did not permit a clear distinction between *iso* and *anteiso* branching in the C-15s and C-17s but a comparison can be made using the ratios of even-numbered saturated acids to the corresponding branched (iso) isomer. Leo and Parker (1966) used this method of comparison in their study of branched-chain acids in sediments and found ratios between 1 and 20 for sediments, compared to ratios between 100 and 500 for organisms studied by Ackman and Sipos (1965). The holothurian gave ratios between 2 and 11 for the C-14, C-16, and C-18 acids, agreeing closely with the sediment ratios and indicating significant enrichment. The holothurian feeds upon the surface layer of the bottom sediments which is known to be rich in organic detritus and bacteria; since bacterial lipids contain large amounts of branched-chain acids (Shorland, 1962) it is probable that these acids in the holothurian are derived from its diet. Leo and Parker (1966) similarly suggested that the branched-chain acids in the sediments might stem from bacterial sources.

The possibility of severe losses of polyunsaturated acids on polyester and nonpolar columns such as reported by Gerson et al. (1966) calls for further investigation. The tests conducted in this study show that the columns are not necessarily always at fault, for arachidonic acid levels matched the known weight per cent within experimental error on both polar and nonpolar columns. Therefore, it is possible that some parameter of operation or detection may be responsible.

TABLE III. Comparison of the fatty acid composition of two holothurians *Scotoplanes theeli* by carbon number as determined on two GLC columns.

Fatty acid carbon no.	Holothurian No. 1 by SE-30 (%)	Holothurian No. 2	
		By DEGS (%)	By SE-30 (%)
12	1.2	0.9	1.9
13	0.9	–	–
14	5.2	2.4	2.7
15	7.0	2.6	3.3
16	19.4	13.0	14.0
17	2.8	2.7	5.0
18	20.3	18.8	18.0
19	–	1.7	tr
20	35.7	44.6	40.0
22	7.5	13.3	15.1

TABLE IV. Fatty acid composition of the holothurian *Scotoplanes theeli*

Fatty acid	Weight per cent
12:0	0.9
13:0	–
13:1	tr
14:br	0.2
14:0	2.2
15:br	1.4
15:0	1.2
15:1	tr
15:2	tr
16:br	0.7
16:0	6.7
16:1	5.6
17:br	0.6
17:0	0.7
17:1	1.2
17:2	0.2
18:br	2.1
18:0	4.3
18:1	10.4
18:2	2.0
19:0	1.7
20:0	1.8
20:1ω9	1.8
20:2ω9	1.5
20:3ω6	tr
20:4ω6	21.2
20:5ω3	18.3
22:4ω6	8.1
22:5ω3	0.4
22:6ω3	4.8

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Differences in Performance of Naturally and Artificially Propagated Sockeye Salmon Migrant Fry, as Measured with Swimming and Predation Tests[1]

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ABSTRACT

Two methods of performance testing were developed to measure differences in stamina in four groups of sockeye migrant fry, all of the Lakelse Lake (Skeena River, B.C.) stock. The four groups differed only in methods of incubation: one group was naturally propagated, the other three artificially. The results of the swimming performance tests and the vulnerability to predation tests agree closely, and analysis shows that the key factor responsible for differences in performance is size of the fish. Ranked in decreasing order of performance these four groups rate as follows: naturally propagated fish, fish incubated in gravel from time of hatching, fish incubated in gravel only for the last few weeks as premigrants, and fish that spent their entire incubation period without gravel in hatchery baskets. Independent of size is the influence of condition (*K*-factor) of the fish, optimum performance occurring at the time of almost complete yolk absorption. Of the two methods the swimming performance test was found to be more sensitive and is recommended as a tool for comparative "quality testing" of fish stocks.

INTRODUCTION

Hatchery fish have been shown in most cases to display a pronounced inferiority to wild fish in survival potential (e.g. Foerster, 1938; Miller, 1954; Wales, 1954; Salo and Bayliff, 1958; Vincent, 1960; and Shearer, 1965). Viability, defined here as capacity for individual survival, comprises many frequently interacting subcapacities, each related to one or more environmental factors such as temperature tolerance, capacities for maximum and sustained swimming speeds, and susceptibilities to predation and disease. (cf. Vibert, 1956, for proposed criteria of viability in salmon and trout). Evidently, no single test other than a lifetime spent under natural conditions can measure viability in toto. There is value, however, in establishing a measure of viability by means of quantifiable tests at a particular stage of the life history, such as the time of release from a hatchery. Such a test amounts to comparative "quality testing" and has a great potential in the increasingly important field of artificial propagation.

Unless extreme conditions can be expected to be severely limiting factors in specific environments, perhaps the generally most important component of viability is stamina. Stamina can be defined as capacity to perform a biological function under specified conditions of exterior and interior milieu;

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this can simply mean swimming against a current or refer to more complex situations, e.g. avoidance of predators, and acquisition of food.

As part of a hatchery evaluation program connected with the operation of an experimental sockeye salmon hatchery at Lakelse Lake, Skeena River watershed, B.C., two methods of testing stamina were developed and carried out at this hatchery on migrant sockeye fry reared under different regimes of incubation. Because swimming performance has been demonstrated to be influenced by many factors (e.g. Bainbridge, 1960) it was chosen for the first testing situation. A second testing situation was desired where swimming performance could be considered an integral part of a more complex relationship that would apply more directly to natural survival, i.e. be of greater biological signifiance. Vulnerability to predation was chosen for this test because it seemed to satisfy both conditions very well. Apart from all other factors that may influence a predator–prey relationship the swimming performance element is related to successful escape from an approaching predator. Predation is further known to be a major factor in the early life history of the free swimming stages of salmon (e.g. Ricker, 1941; Roos, 1960).

Our swimming performance and predator tests are concerned with two different, but related, types of performance: the first is a measure of "sustained swimming" capacity over relatively long periods of time, whereas the second test depends, in addition to other possible factors, more directly on "burst swimming" capacity, i.e. a sudden burst of maximum performance only lasting a fraction of a second; pursuit over any distance was rarely observed in the tests.

MATERIALS AND METHODS

All tests were carried out with progeny of adult sockeye salmon of the stable Lakelse Lake population, which has been naturally propagated for the last 25 years up to and including the time of these experiments. Tests were performed on fish of two brood years, 1962 and 1964. Four groups of fry were used, differing in incubation treatment as follows.

Group 1. The "wild" fry. These were obtained with trap nets from the natural fry run in Williams Creek, the creek utilized by the parent fish.

Group 2. The "hatchery" fry. In 1963 these fish were taken from the production run of the hatchery. They were incubated in Burrows-type baskets and trays to an advanced alevin stage. Roughly at the time pigmentation of the sides had advanced to about half the height of the fish, they were moved to large gravel-bottomed release tanks where they completed their development. From these tanks they released themselves by swimming to the surface and were carried by overflow into a flume to the creek. Samples were obtained from the flume. In 1965 hatchery-production fish were not available, but a battery of eight experimental release tanks produced fry very similar to the production-run fish. These fry were also procured when they released themselves.

Group 3. The "basket" fry. These were fry that completed larval development inside an incubation tray. Having no means of releasing them-

selves, they were taken from the trays when they had reached a stage of development comparable to that of self-releasing hatchery fry. Many of these fish had, at this time, achieved neutral buoyancy, as is characteristic of the migrant-fry stage.

Group 4. The "gravel" fry. These were fish raised in experimental incubation troughs in which the alevins upon hatching in a wire basket dropped into a bed of gravel, where they completed their development. They released themselves by migrating from the gravel to the surface, whence they were carried from the trough by an overflow. Samples were taken from the overflows.

The outstanding difference between the four groups at time of migration was in their average size. For any one release (migration) date they ranked as follows: wild > gravel > hatchery > basket.

The fry of all groups reached the migrant-fry stage at very similar stages of development. Morphologically this stage is normally characterized, as was the case with our samples, by the closing of the "ventral slit," which is the transparent window along the ventral median caudad of the pectoral fins, consisting of an area of as yet unpigmented abdominal wall, delineated by the edges of the advancing pigmentation that already covers the rest of the body. Complete closure closely coincides with an almost complete absorbtion of the yolk reserve. This stage is characterized by a drastic change in behaviour. During the in-gravel, premigrant period the fish are quiescent, negatively phototactic, and cover-seeking. In the migrant stage they are active, negatively thigmotactic, and surface-seeking until they achieve neutral buoyancy; then they become pelagic, and, in light, they show a positive rheotactic response and start feeding. The incubation period is now completed and, what is important to our investigation, the period of hatchery influence is terminated, so that any differences in survival potential that may exist between groups that were treated differently are now "built into" the fish and should be available for analysis.

All fish were held at the hatchery in troughs or holding tanks under ambient conditions of temperature, oxygen levels, and other factors, as determined by the hatchery's water source, Scully Creek. Groups that were tested simultaneously were collected on the same day and held under identical conditions. Unless specifically mentioned, the fry were not fed and the amount of foodstuffs carried in with exchange water was negligible. Where necessary, fish were differentially marked by partial removal of one ventral fin, the left in one group, the right in the other, after narcotizing to immobility in 2-phenoxy–ethanol. There was no mortality in control groups held in aquaria at the hatchery for 48 hr after clipping and handling.

SWIMMING PERFORMANCE TESTS

Materials and Methods

Swimming performance is a form of expenditure of labour, i.e. energy in time. Any measure of *absolute performance* must be obtained from accurate

measurement and/or tight control of these factors, and a number of others as well, that affect the energy supply and delivery systems. Obvious examples are immediate past history of the fish and ambient temperature and oxygen levels. Unless tests that are separated in time and space are rigidly controlled and performed under truly comparable conditions, direct comparison of absolute performance data is, at best, of doubtful value.

For groups of fish that are simultaneously available a much simplified procedure can be employed that accurately measures *relative performance* and not only establishes the existence of differences in swimming performance between groups, if such exist, but also quantifies those differences in relative, but comparable, terms. The procedure involves simultaneous testing of two (or more) groups of fry under identical conditions, such as can be achieved by testing both groups at once in the same apparatus, but does not require accurate control or measurement of the actual conditions as long as they are generally favourable to a proper functioning of the animals. The method uses for the measured response not actual performance time under a certain water-velocity regime, but only the *ranking order* in which the individuals of both groups during each test reach a stage of fatigue at which they fail to maintain themselves in the current and drop out. This ranking order determines exactly the relative position of each fish of either group in one continuous series of increasingly superior swimming performance. The method for treatment of these ranking data is given further on under Analysis of the Data.

Evidently a comparison between the two groups of each test is valid because during the test all factors are identical at all times for both groups irrespective of whether they are controlled or are allowed to vary. Comparability between tests, however, becomes questionable under the latter conditions. It is the great advantage of this relative method that *under varying conditions valid comparisons can be made.* This is of special importance in field situations, where rigid environmental control is not usually feasible. The comparability ensues from the assumption that a limited degree of variation in test conditions which would affect absolute performance does not affect relative performance, i.e. a certain change in conditions may affect the fish adversely and reduce their absolute performance but, because it affects all fish similarly, it does not alter the relative position of each individual in the ranking order. Therefore, with the ranking order as response, there is no need for rigid control over the environment as long as the conditions are similar between tests. The same applies to the factors water velocity and duration of effort: their regimes only need be similar in all tests that are to be compared and their absolute values need not be known. The validity of the assumption seems assured especially in case of nearly identical or closely related groups of fish where physiological requirements and tolerance ranges are likely to differ but little if at all.

The design of the test flume is illustrated in Fig. 1. The experimental area measured about 30 × 75 cm. In the earlier series of tests (in 1963) the

FIG. 1. Performance test flume. 1, flow controlling valve; 2, water inlet; 3, flow regulating and cleaning screens; 4, upstream brass retaining screen; 5, plate glass sides and bottom; 6, plate glass center partition; 7, electrified grid; 8, downstream brass retaining screen, also serves as second electrode; 9, water level during test; 10, movable wooden sill controlling depth and flow; 11, wooden trough, built of 2-inch planks.

trough was divided lengthwise into two equal compartments with a vertical glass plate; in 1965 no partition was used.

It proved necessary to reinforce the normally fairly strong tendency of the fry to display spontaneous positive rheotaxis in the trough. Many fish developed an escape behaviour in continuing strong water currents long before they were physically exhausted. It was also found that some fish would fall back on the downstream screen, sometimes remain there for a considerable period of time, and then resume swimming. To avoid these complications to the procedure, an electrical charge was introduced between the downstream brass screen and a second metal grid suspended approximately 25 mm in front of it. The final design used a 60-cycle a-c voltage that was obtained from the "neutral" side of the coil of a variable Powerstat transformer.

A training period involving not less than 12 hr at 4 v between the grids was sufficient for the fish to learn to avoid the screen and to move away from it during the subsequent test if they drifted slowly toward it. Shorter learning periods were effective in achieving complete avoidance at low water velocities but proved ineffective at higher velocities, when the fish upon stimulation by the field would reverse their rheotactic orientation and attempt to escape with a fast dash downstream. It was found necessary to increase the voltage to 25–30 v during the test to prevent fish from coming back through the field and reentering the experimental area. This higher voltage also enabled trained fish to sense the field farther upstream, at least 5 cm ahead of the grid, a desirable feature that facilitated avoidance. To aid orientation within the trough a small bright light was located just above and in front of the grids, a cover was placed over the forward end of the experimental area, and contrasting stripes were chalked on the sides and bottom of the trough behind the plate-glass liners.

During the series of tests in 1963 the two groups of fry that were to be tested simultaneously were kept separate by placing one group in each of the two compartments of the trough. The two groups contained the same number of fry. The trough was located outdoors. Upon introduction, the fry were left at a very low water velocity (not more than 15 mm per second) for a minimum of 12 hr. The rate at which the fish dropped out after the water velocity was increased proved to decrease exponentially and, to get all the fish out in a more or less regular sequence within a few hours, it was necessary to increase the flow at intervals. The flow was increased whenever about 5 min elapsed during which time no fish dropped out and all remaining fish were swimming strongly and well ahead of the grid. No more than 10–12 fish per compartment could be used; if larger numbers were put in, there was a tendency for fish that were not yet fatigued to drift into the electrical field together with some fatigued fish as a result of strong schooling behaviour.

In 1965 several shortcomings in technique were corrected. The trough was taken indoors, eliminating many disturbing stimuli such as changing light patterns and wind ripples that hampered earlier tests. To reduce further any bias due to unequalness of the two sides of the trough, the partition was

removed. The fish were marked differentially for recognition of source (see page 1119, paragraph 4, under Materials and Methods). Under the new conditions it proved feasible to at least double the number of fish in the tests. Schooling behaviour still caused some fish to drop out prematurely, but to a much lesser extent than in the outdoor tests. If a fish dropped out while actively swimming downstream, e.g. in chasing a food particle, it was omitted from the analysis.

For tests where individual fork lengths[2] and body weights were required, the fish were recovered as soon as they passed through the electrical field, killed with an electric shock, and laid out flat on numbered squares between layers of filter paper soaked in 5% formaldehyde solution. Measurements were usually carried out the following day. All measurements on fish from one experiment were done in quick succession to ensure comparability within the experiment.

Analysis of the Data

1. Two-group tests (s-1 to s-5)

All fish of both groups of each test were ranked in a single series in order of dropout (ODO) and consecutively numbered from 1 through $[n_1 + n_2]$, where n_1 = number of fish in group 1 and n_2 = number of fish in group 2. For each group the rank values were totalled, R, and the average value for the group ($\mu R = \frac{R}{n}$) was calculated. The difference between the rank means $(\mu R_2 - \mu R_1)$ is a quantitative measure of the difference in performance of the two groups.

However, the value of this statistic is sample-size dependent. To permit direct comparison between tests that use different numbers of fish the difference in rank means was therefore transformed to

$$\left.\begin{aligned} d_R &= \frac{(\mu R_2 - \mu R_1)_{\text{test}}}{(\mu R_2 - \mu R_1)_{\text{max}}} \cdot 100 \\ (\mu R_2 - \mu R_1)_{\text{max}} &= \frac{n_1 + n_2}{2} \end{aligned}\right\} \quad d_R = \frac{2(\mu R_2 - \mu R_1)}{n_1 + n_2} \cdot 100$$

which expresses the difference as a percentage of the maximum difference that could occur in that test. A d_R of 0% thus indicates identical performance of the two groups (uniform interdigitation of the two groups in the ranking series) and 100% indicates maximally different performance (complete separation of the two groups).

The statistic d_R is numerically very descriptive of the measured differences in performance, for which purpose it was indeed developed, but it lacks the

[2]Bainbridge uses *total* length, which is perhaps a closer approximation to the physiological concept of *propulsive* length. The difference is of no concern to our relative method.

properties necessary to establish probability levels connected with the differences. For this purpose a related statistic, U, as used in the Mann-Whitney U-test (Siegel, 1956), was employed. The sampling distribution of U under the null-hypothesis is known. U is based on the number of times a score in one group is preceded by a score in the other group and can be expressed as

$$U = n_1 \cdot n_2 + \frac{n_1(n_1 + 1)}{2} - R_1$$

where n_1 and n_2 are the numbers of fish in each group, and R_1 is the sum of the ranks assigned to group 1. U is directly related to the difference in rank means ($\mu R_2 - \mu R_1$) and significance levels established for U are thus equally valid for both statistics. To see this we can write the equation for U as $(a - R_1)$ where a is a constant for each test, being determined by n_1 and n_2 only; and ($\mu R_2 - \mu R_1$) can be written as

$$\left[\frac{\frac{1}{2}(n_1 + n_2)(n_1 + n_2 + 1) - R_1}{n_2}\right] - \left[\frac{R_1}{n_1}\right] = \frac{(b - R_1)}{c} - \frac{R_1}{d}$$

where b, c, and d are constants determined by n_1 and n_2 only; hence the value of both statistics varies directly with R_1. The p-values cited in text and tables are the probabilities of values as large as the established differences occurring between the rank means if the samples were taken from two populations with the same rank mean. Probability values for a two-tailed test are desirable for the earlier experiments but to be precise this is not realistic for the later experiments (test 21 et seq.) because the outcome of these was predictable on the basis of the earlier tests. However, to evaluate all tests on their own merits, and further to facilitate comparison, the higher two-tailed values were adhered to throughout, unless specified otherwise.

The Kendall rank correlation test (Siegel, 1956) was employed for determination of correlation between length and order of dropout in series S-4 and S-5. Its statistics (τ)ranges from zero for no correlation to unity for perfect correlation. Probabilities are given for the one-tailed test because the direction of correlation was predictable.

2. SINGLE-GROUP TESTS (S-6 AND S-7)

In series S-6 the degree of agreement was determined between an empirically established relationship between length and order of dropout for each of five tests, and a corresponding theoretical relationship evolved from the hypothesis that the order of dropout is determined by the differences of length as these are observed in the experimental population. The empirical relationship was calculated by ranking the fish of each test in *order of dropout*, dividing this series into equal classes (e.g. 1 to 10, 11 to 20) and calculating the average length for each of these classes. The hypothetical relationship was established by the reverse procedure, viz. the same group of fish was ranked in *order of*

increasing length, the resulting series was divided into the same number of "length" classes each containing the same number of individuals as in the order of dropout ranking, and the expected order of dropout was calculated. The fry were not evenly distributed for length over the experimental populations. This was reflected in a varying size-range occurring in the successive "length" classes of the hypothetical relationship that were limited to a constant number of fish, n, each. This variation in size-range resulted in an irregular, nonlinear relationship between length and order of dropout. A straight line for this hypothetical relationship would facilitate comparison greatly and would occur if these successive "length" classes each spanned the same size-range. A method (Table VI) was developed to adjust the data to obtain this straight line relationship. The average length obtained in each "length" class of n fish of the hypothetical relationship (C.V. in Table VI) was adjusted to the value this class of n fish would have had if the population had been evenly distributed for length, i.e. had consisted of n fish in each of the required number of length classes of equal size range (A.V. in Table VI). To adjust the empirical relationship to the same distribution, the same length increments (d in Table VI) that were added or subtracted to the successive "length" classes were now added to or subtracted from the calculated average lengths of the successive order of dropout classes so that the two relationships were again comparable.

To test for degree of correlation and its significance, the Kendall rank correlation test was employed. Because this test is based on ranking order, and this order in the unadjusted data was distorted by varying ranges of the length classes, the test was run on the adjusted data where the length classes span equal intervals.

Results and Discussion

The results are arranged in seven series, each relating a number of similar tests. The first five series concern measurements of differences in performance between two subject groups that differ in incubational treatment, or some other characteristic. The sixth series concerns the effects of length investigated as a single continuous variable in each test. The seventh, and last, series deals with the effect of condition (K-factor) on performance, and other sources of variability.

S-1: *Hatchery-produced versus naturally produced fry.* — Five tests on random samples from the two groups were carried out in both 1963 and 1965. In all comparable tests "wild" fish performed better than "hatchery" and "basket" fish (Table I).

Tests 5 and 6, and 7 and 8 are pairs of observations in a biased trough. Because the locations of the groups were reversed during the second test of each pair, the corresponding unbiased d_R values are approximated by averaging the values for each pair.

Tests 22 and 23, run in 1965 on hatchery fry in good condition, are comparable with the 1963 tests when the fry were in similar good condition. Their average $\bar{d}_R$ of 48.5% is similar to the average $\bar{d}_R$ of 50.1% obtained in 1963.

TABLE I. S-1. Differences in swimming performance between random samples of "hatchery" and "wild" fry (tests 5–23), and "basket" and "wild" fry (tests 29–30), as shown by the order in which they failed to maintain their position in a current.

	Source 1		Source 2				
	Hatchery or basket		Wild				
Test[a]	Cdn_1	n_1	Cdn_2	n_2	d_R (%)	p	$\bar{d}_R$ (%)
5	G	12	G	12	23.6[b]	.45	
6	G	12	G	12	75.7[b]	.001	
7	G	12	G	12	18.6[c]	.65	50.1
8	G	12	G	12	75.0[c]	.001	
9	G	12	G	12	57.6	.018	
21	F	25	PP	25	−37.0	.0248	−37.0
22	G	25	G	25	40.5	.0014	48.5
23	G	25	G	25	56.5	< .0003	
29	G	24	G	25	62.2	< .00022	72.1
30	G	25	G	25	92.1	< .00001	

[a]Tests 1–20 were carried out in 1963; 21–30 in 1965. All tests are consecutively numbered as executed, irrespective of series.

Cdn = condition. G = good, near optium, little yolk left; F = fair, below optium, no yolk left; P = poor, approaching emaciated state; PP = very poor, emaciated.

n = number of fish of each source used for analysis.

d_R = measure of difference in performance, expressed as $\frac{2(\mu R_2 - \mu R_1)}{(n_1 + n_2)} \cdot 100$

d_R-values in parentheses indicate unreliable tests.

p = two-tailed probability of U (and d_R) occuring under H_o

$\bar{d}_R$ = average d_R for indicated group of tests.

[b,c]Corresponding pairs in biased trough.

Tests 29 and 30, carried out on the smaller "basket" fish and "wild" stock, showed an even more pronounced difference in performance: the d_R values were 62.2 and 92.1% respectively, and averaged 72.1%.

Test 21 stands by itself in that it used fry that were in poor condition. For this test both groups were collected on the same day and then held, unfed, in aquaria. The test was run when the wild fry had used up all their yolk and were rapidly becoming emaciated ("pinheads"), whereas the hatchery fry, which started out with a little more yolk, were still in good shape. The hatchery fry performed considerably better than the wild fry (d_R = −37%) but all performed less well than the hatchery fry in good condition: maximum water flow during this test was of the order of four body-lengths per second only, as opposed to six to seven body-lengths per second for fry in better physical condition. The results of this test indicate that the production of thin or pinheaded fry (a common problem in some hatcheries) imposes a

serious handicap on the stock. Further information on the effect of condition on performance is related on p. 1135 MS *et seq.*

S-2: *"Basket" fry versus "gravel" fry.* — Two tests were carried out on fry of these sources (Table II). In both tests the gravel fish performed better than the basket fish.

Test 27 was an exceptionally "good" test with most fish dropping out when visibly fatigued. This reduced the variability within the experiment and increased the rank difference; compared with "normal" tests its d_R value is high. Test 28 was an unusually "poor" test with many fish dropping out before being fatigued. This had the opposite effect on the d_R value obtained; the average of the two tests, 45.2%, is therefore a more realistic figure than the individual values in relation to the other tests. This difference in performance is closer to that between "wild" and "hatchery" fry than that between "wild" and "basket" fry. Gravel fry were not tested directly against wild fry.

S-3: *Selected "hatchery" fry in good condition versus "wild" fry in below-optimum condition.* — Six tests were run in 1963 comparing samples of naturally propagated fry that were of below-optimum condition but with a "normal" length distribution with groups of "hatchery" fry selected by eye for large size and good condition (Table III). The selected "hatchery" fry showed a consistently superior response.

During the series the average condition of the wild fry deteriorated from reasonably good to poor. The hatchery fish, which were collected on the same day as the wild stock, had more yolk reserve and the increasingly better relative performance of the hatchery fry was largely attributable to an increasingly poorer absolute performance of the wild fry. It would appear that if both groups of fry had been tested earlier, when both were in very good condition, performance would have been very similar.

Tests 12 and 13 (d_R = −36% and −20%) were unreliable. Schooling behaviour caused groups of fish to drop out simultaneously which may or may not have included some fish that were not close to exhaustion yet.

S-4: *Large "hatchery" fry versus small "hatchery" fry.* — For this series of five tests, hatchery fish from the same release date were sorted by eye for

TABLE II. S-2. Differences in swimming performance between random samples of "basket" fry and "gravel" fry, as shown by order of dropout. See Table I for explanation of symbols.

	Source 1		Source 2				
	Basket		Gravel				
Test	Cdn_1	n_1	Cdn_2	n_2	d_R (%)	p	$\bar{d}_R$ (%)
27	G	24	G	25	($\leq$63.7)	< .0002	(45.2)
28	G	24	G	25	($\geq$26.7)	< .13	

TABLE III. S-3. Differences in swimming performance between "hatchery" fry selected for size and random "wild" fry, as shown by order of dropout. The wild fry were in increasingly below-optimum condition. See Table I for explanation of symbols.

	Source 1		Source 2				
	Large hatchery		Random wild				
Test	Cdn_1	n_1	Cdn_2	n_2	d_R (%)	p	$\bar{d}_R$ (%)
10	G	12	G	12	−24.9	.55	
11	G	12	F	12	−25.0	.42	
12	G	12	F	12	(−36)	(.25)	−33.3
13	G	12	F	12	(−20)	(.6)	(33.5)
14	G	12	P	12	−50.0	.044	
15	F	12	P	12	(−45)	(.04)	

size. The larger fish consistently outperformed the smaller fish and a generally increasing d_R was indicated with increasing size differential. The extent and significance of this apparent relationship was determined with the Kendall rank coefficient test which indicated a partial correlation, $\tau = +0.60$ ($p = 0.117$).

S-5: *Large fry versus small fry from various sources.* — The fry of tests 25 through 30 can be divided into two groups, a "smaller" and a "larger" half of the experimental population, while disregarding source, to obtain additional information on the effect of length on performance (Table V). All six tests used a mixture of fry from two or three sources. The results confirmed the positive relationship between length and performance at much higher levels of significance than in S-4.

With the exception of test 27, which as previously explained shows an inflated d_R value due to an unusually small variability, an increasing d_R with increasing size differential is evident. For the five remaining tests, $\tau = 0.8$ ($p = 0.042$). If test 28, which has a low d_R value due to premature dropouts, is also excluded, τ becomes unity ($p = 0.042$).

Figure 2 shows the results of S-4 and S-5 graphically. The slope relating d_R to length differential obtained in 1965 (S-5, all data) differs markedly from the slope obtained in 1963 (S-4, all data). This reflects, in all probability, the difference in accuracy (variation level) between the two different techniques. It is noteworthy that test 27 with its unusually low variance stands out by itself whereas test 28 with its increased variance due to schooling-induced premature dropout aligns closely with the 1963 experiment when early dropouts were a continuing problem. However, because the fry of each source were not equally divided over both length-groups in each test of S-5 the effects of length may be confounded with other source-induced factors. These factors

TABLE IV. S-4. Differences in swimming performance between small and large "hatchery" fry, as measured by order of dropout. Fork length measurements in mm. d_l = length differential in mm. For further explanation of symbols see Table I.

	Source 1, small				Source 2, large						
Test	Cdn_1	n_1	$\bar{L}_1$	$Range_1$	Cdn_2	n_2	$\bar{L}_2$	$Range_2$	d_l	d_R (%)	p
18	G	10	26.0	24.0–27.0	G	10	29.8	28.0–31.5	3.8	55.0	.045
16	G	10	27.7	25.5–29.5	G	10	31.3	30.5–33.0	3.6	(39.0)	–
20	F	6	26.7	25.0–28.0	F	8	29.8	28.0–31.0	3.1	29.3	.414
17	G	10	27.0	24.5–29.0	G	10	29.5	28.5–31.0	2.5	23.0	.52
19	G	10	27.1	24.0–29.0	G	10	29.4	28.0–30.5	2.3	34.6	.26

Correlation between length differential (d_l) and performance differential (d_R) as measured with a Kendall rank correlation coefficient: $\tau = +0.60$ ($p = 0.117$).

TABLE V. S-5. Differences in swimming performance between small and large fry of different, mixed origins, as measured by order of dropout. Fork length measurements in mm. d_i = length differential in mm. For further explanation of symbols see Table I.

	Source 1, small				Source 2, large						
Test	Cdn_1	n_1	$\overline{L_1}$	$Range_1$	Cdn_2	n_2	$\overline{L_2}$	$Range_2$	d_i	d_R (%)	p
30	G	25	25.7	22.8–27.6	G	25	29.8	27.6–31.0	4.1	92.1	<.00001
29	G	25	26.5	25.0–27.6	G	24	29.8	28.0–31.8	3.3	62.2	<.00022
26	G	41	26.2	24.4–27.0	G	39	28.9	27.2–31.0	2.7	52.8	.00006
28	G	24	25.9	25.2–26.6	G	25	27.9	26.8–28.8	2.0	(>)25.1	.1336
25	G	34	26.0	24.6–26.8	G	33	27.9	27.0–29.4	1.9	33.0	.0102
27	G	25	25.4	24.2–26.2	G	24	27.2	26.4–28.4	1.8	(<63.1)	<.0002

Excluding test 27 the Kendall rank correlation coefficient, $(\tau) = +0.80$ ($p = 0.042$). Excluding tests 27 and 28, $(\tau) = +1.0$ ($p = 0.042$).

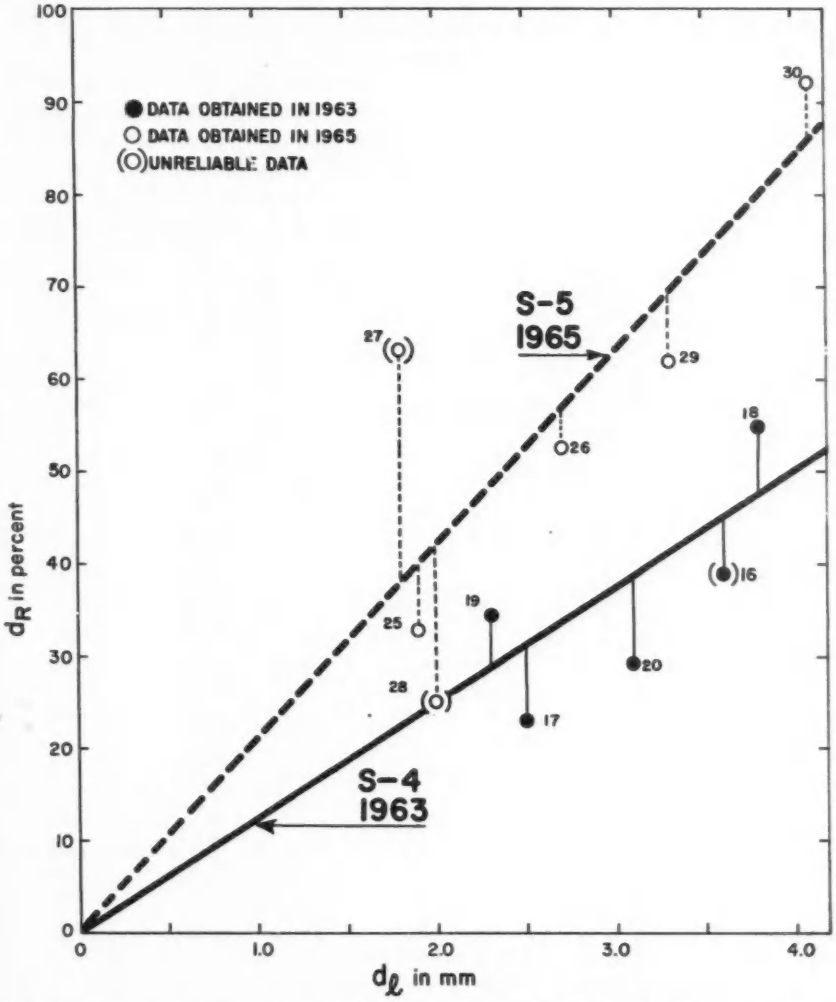

FIG. 2. Relationship between length differential (d_l) and rank of swimming performance differential (d_R) in groups of fry. S-4: all fry of one source (hatchery); S-5: groups are mixtures from two or three sources (wild, gravel, hatchery, basket). Numbers are test numbers.

could not have been present in S-4, because both length-groups were from the same source.

S-6: *Relationship between length and order of dropout.* — In this series of five tests the hypothesis was tested that, when the condition of the fish is held constant, differences in order of dropout are largely attributable to differences in lengths only. The results were as follows.

TABLE VI. Procedure of correction for uneven distribution. Test 26, compare with Fig. 3a.

Arbitrary length-class value:		(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)						
Available number per length-class:		2	13	19	17	8	12	6	2	Σ	C.V.	A.V.	d	Data uncorrected	Data corrected
Actual make-up of each class	1	2	8	–	–	–	–	–	–	10	1.8	1.0	+0.8	25.8	25.0
	2	–	5	5	–	–	–	–	–	10	2.5	2.0	+0.5	26.7	26.2
	3	–	–	10	–	–	–	–	–	10	3.0	3.0	0	27.0	27.0
	4	–	–	4	6	–	–	–	–	10	3.6	4.0	−0.4	27.1	27.5
	5	–	–	–	10	–	–	–	–	10	4.0	5.0	−1.0	27.4	28.4
	6	–	–	–	1	8	1	–	–	10	5.0	6.0	−1.0	27.4	28.4
	7	–	–	–	–	–	10	–	–	10	6.0	7.0	−1.0	28.5	29.5
	8	–	–	–	–	–	1	6	2	9	7.1	8.0	−0.9	29.5	30.4

Actual class value (C.V.) calculated as average of sum of products of numbers actually present in each length-class times arbitrary class value. Example: Class 6: $\frac{1 \times 4 + 8 \times 5 + 1 \times 6}{10} = 5.0$. Because the arbitrary value (A.V.) for this class is 6.0 the differential (d) is −1.0. As each length-class was chosen, in this case, to include 10 mm, the addition of 1.0 × 10 mm to the empirical data for the sixth class order of dropout (Data uncorrected, 27.4) now gives the corrected value (Data corrected, 28.4).

The tests (Table VII and Fig. 3) were run on groups of fry each consisting of a mixture of fry from different sources but of comparable condition to determine the degree of agreement between a hypothetically expected and an empirically established relationship between size and order of dropout. The method is explained under 2. Single-group tests (S-6 and S-7). "Condition" was estimated by eye on morphological characteristics (ventral slit) in the

TABLE VII. Average lengths for successive classes of dropouts, empirical and hypothetical. d_p = differential between experimental (corrected) and expected (hypothetical) values for length-class averages; τ = Kendall rank correlation coefficient for grouped corrected data; p = probability of chance occurrence of τ under H_0.

Test and source	ODO class	Average fork length (*mm*)			d_p	τ	p
		Data	Corrected	Expected			
26	1–10	25.8	25.0	24.4	+0.6		
	11–20	26.7	26.2	25.4	+0.8		
	21–30	27.0	27.0	26.4	+0.6		
Basket	31–40	27.1	27.5	27.4	+0.1		
Gravel	41–50	27.4	28.4	28.4	0		
Wild	51–60	27.4	28.4	29.4	−1.0		
	61–70	28.5	29.5	30.4	−0.9		
	71–80	29.5	30.4	31.4	−1.0	0.96	< .0001
27	1–10	25.3	25.0	24.4	+0.6		
	11–20	25.6	25.2	25.4	−0.2		
Basket	21–30	26.4	26.4	26.4	0		
Gravel	31–40	28.6	27.2	27.4	−0.2		
	41–49	27.4	27.9	28.4	−0.5	1.0	.0083
28	1–9	26.0	25.1	24.4	+0.7		
	10–18	26.4	25.4	25.4	0		
Basket	19–27	26.5	25.9	26.4	−0.5		
Gravel	28–36	27.2	27.2	27.4	−0.2		
	37–45	26.8	27.5	28.4	−0.9	1.0	.0083
29	1–7	27.0	26.7	25.4	+1.3		
	8–14	25.9	25.9	26.4	−0.5		
	15–21	28.0	28.4	27.4	+1.0		
Basket	22–28	27.8	28.4	28.4	0		
Wild	29–35	28.2	28.2	29.4	−1.2		
	36–42	29.6	30.0	30.4	−0.4		
	43–47	31.0	31.4	31.2	+0.2	0.66	.022
30	1–7	25.0	24.6	24.6	0		
	8–14	25.5	25.1	25.6	−0.5		
	15–21	26.3	26.0	26.6	−0.6		
Basket	22–28	28.3	27.1	27.6	−0.5		
Wild	29–35	29.5	28.5	28.6	−0.1		
	36–42	30.2	29.3	29.6	−0.3		
	43–46	30.3	30.3	30.4	−0.1	1.0	.0002

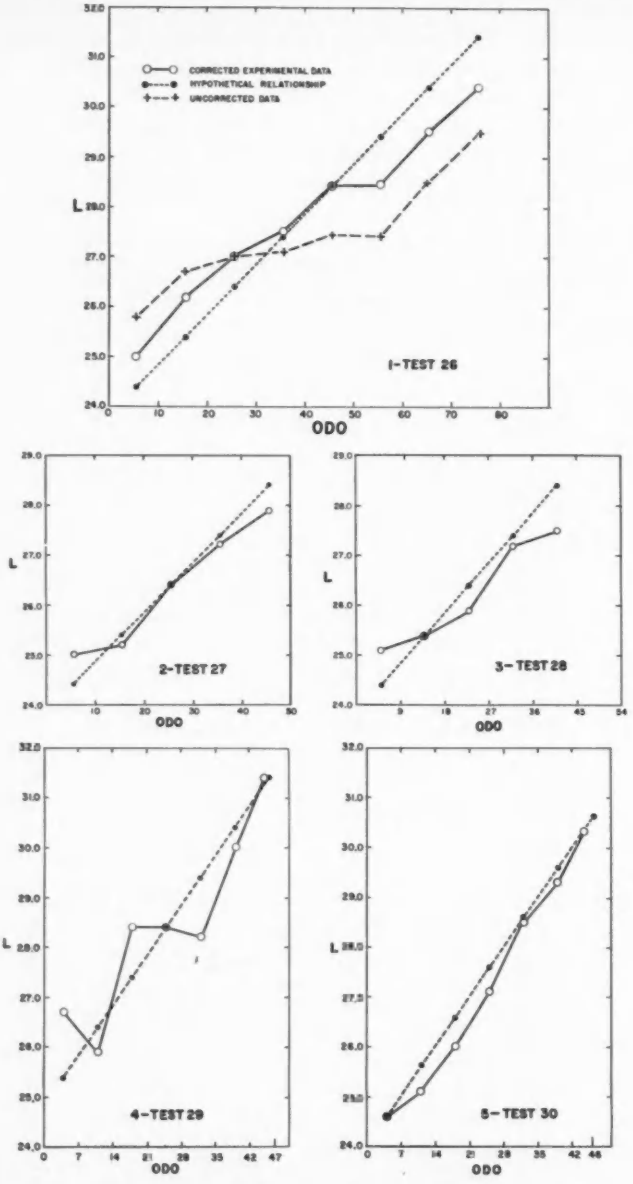

FIG. 3. Empirical and hypothetical relationships for five tests between length (L) and performance (as order of dropout, ODO) in migrant frv. The empirical relationships relate average lengths of successive groups of dropouts as established in a test; the corresponding hypothetical relationship is generated by assuming the fish of the same population to dropout in order of increasing length. Both relationships are corrected for distribution.

selection of comparable samples. In tests 27 and 30 the corrected data conformed very closely to the expected line. The variation in order of dropout for each length-class in these tests was small. In tests 26 and 28 the corrected data show the expected straight lines but with a slightly lesser slope than expected. Variation in these tests was greater than in tests 27 and 30, and probably accounts for the small decrease in slope, because it decreases the average length of the fish making up the last ODO class and increases the average length of the fish in the first ODO class; in midrange the effect cancels itself. The results of test 29 are in general agreement with the other four tests, but large deviations are evident in the first, third, and fifth ODO class. These deviations cannot readily be attributed to a factor, other than length, that affected performance; a scatter diagram of the data (length over order of dropout) clearly indicated that the extreme values of ODO classes 1, 3, and 5 were mainly due to an odd chance distribution.

Except for test 29, the correlation between length and order of dropout was high ($\tau \geq 0.96$) and significant ($p \leq 0.0083$) in all tests. The conclusion is warranted that for the individual fish of the four groups of fry tested, difference in length (or some factor(s) directly related to length) was the key factor in effecting considerable differences in swimming performance.

The effect of length on swimming performance is well documented in the literature for several species including sockeye (yearlings) (cf. Bainbridge, 1958; Vincent, 1960; Brett et al., 1958; and Green, 1964).

Of special concern to our project is the cause of differences in performance between groups of fry with different incubation histories. Having established the correlation between performance and length for *individual fish*, the question arises whether the differences in size between the *groups of fish* of different sources do fully account for the differences in performance of these groups. The tests of series S-3 employed groups of "wild" and "hatchery" fish of comparable length distributions, but the results were confounded with differences in condition between the two groups. Extrapolation of the results indicated that performance would have been similar if condition of the fish had been similar. Unfortunately, no other direct measurements are available. However, with some of the later tests we can obtain a measure of the degree of influence of length on the difference in performance by comparing a ranking analysis by length that disregards source with an independent ranking analysis by source that disregards length. By subtracting the d_R value obtained for the first (average effect of length only) from that obtained for the latter (absolute effect of source only), we obtain the combined effect of all factors except length that are related to source.

A difficulty occurs because the division into two groups by length does not fully disregard source because the fry of each source are not equally divided over both length-groups. This is unavoidable because variations in length are source induced and the samples were not selected for length. However, if an area of overlap exists, the method is effective on this segment of the experimental population. When all fish are used a difference will still be found if an

extensive area of overlap exists and the effect of factors other than length is large.

Unfortunately, only two tests, 27 and 28, show sufficient overlap in length in the two groups of fry to allow this method to be used effectively. In the ranking analysis by length (S-5) d_R was 63.1 for test 27, and 25.1 for test 28. In the ranking analysis by source (S-2) d_R was 63.7 for test 27, and 26.7 for test 28. The differences, 0.6 and 1.6% respectively, are consistent in both tests and in favour of the "gravel" fish but very small in comparison with the effects of length, and statistically highly insignificant.

Tests 29 and 30 have insufficient overlap to yield any information with this technique. Inspection of scatter diagrams (length and source over order of dropout) for these two tests showed no trends indicating any effect other than that caused by length.

From these analyses it is concluded that no source-induced factors other than length affected relative performance significantly in the fry groups investigated providing the fish were of similar condition.

S-7: *Factors other than length responsible for variation in order of dropout.* — As observed in tests 26 through 30 a large variation in order of dropout occurs in any one length-class. This seems to be a common occurrence with swimming performance tests and various causes have been postulated in the literature. For example, Bainbridge (1960, p. 135) says, "It (the variation) may be accounted for by the possession of a more phlegmatic temperament or perhaps by the one fish being in poorer condition than the other." Vincent (1960, p. 42) remarks that "deviations from mean swimming time were fairly wide," and from his histogram, Fig. 6, three- to fourfold differences in swimming time at a given size are evident. He names only the testing trough as a possible source. He quotes Radcliffe (1950) as also experiencing wide standard deviations.

In our tests varying condition of the fish proved to be partly responsible for the variation in performance. Condition is expressed here as $K = \frac{10\sqrt[3]{\text{weight in mg}}}{\text{length in mm}}$. Because we are dealing with unfed fry at developmental stages that involve yolk absorption the use of the K-factor is not fully comparable to its use for older feeding fish. A high K-value indicates here a fish with considerable yolk reserve. The K-value drops with progressing yolk absorption. Once the yolk is fully absorbed the two uses become comparable because the fry now resorb body fats and other tissues and become increasingly emaciated.

From previously related tests (test 21 in S-1, tests 10 to 15 in S-3) it is evident that after unfed fry pass through the stage of total yolk absorption, stamina rapidly decreases so that fish of a certain (good) condition out-perform fish of similar or greater length that are in poorer condition.

It seems likely that an optimum condition exists because at stages before total yolk absorption the protruding yolk sac constitutes an obvious hydrodynamic disadvantage requiring an increase in effort to stem a current; this can be readily observed if tailbeat frequencies and amplitudes are compared.

Tests 3 and 4 (Table VIII) were run on two groups each of hatchery fry selected for similar length but differing considerably in yolk content, and this effect was demonstrated. In each test one group consisted of fully "buttoned up" fry with little yolk content; the other group of fry in test 3 had a pronounced ventral slit and those in test 4 had a very wide slit, indicating considerable yolk reserve. Even though these early tests were seriously hampered by schooling effects that drastically reduced the difference in performance as measured, a pronounced reduction in performance was evident with increasing yolk content.

It is concluded that the condition (K-factor) of unfed migrant fry affects swimming performance as follows: on both sides of an optimum value, which lies close to the stage of almost total yolk absorption, swimming performance of fish similar in length decreases in direct relation to the deviation of K from the optimal value. One would expect performance to decrease "exponentially" on both sides of the optimum (not necessarily symmetrically) and the line relating performance to condition to be dome-shaped with its maximum at

TABLE VIII. S-7. Differences in swimming performance between similar sized "hatchery" fry of different conditions (K-factor), as measured by order of dropout. K-values higher than "normal" refer to fry having considerable yolk reserve, ventral slit not yet closed.

Test	Source 1		Source 2			
	K	n_1	K	n_2	d_R (%)	p (1 tailed)
3	>normal	22	=normal	25	14.9	.096
4	Much >normal	20	=normal	20	28.8	.06

the optimum K-value. Consequently, considering a group of fish of an experimental population that show similar performance, the expected relationship between length and condition of the fish in that group will also be dome-shaped, i.e. small fish in optimal condition, larger fish in more extreme condition, and the largest fish in the most extreme conditions all show similar performance. This relationship (Fig. 5C) is of great importance to proper assessment of swimming performance data.

Attempts to confirm and to establish more accurately the shape of this relationship with the individual length and weight data obtained in tests 26 to 30 were frustrated by two conditions of these experiments. *1.* In the five experimental populations the variation of K was limited, its distribution being skewed or only covering one-half of the possible distribution, i.e. from the optimum down or up only. *2.* The order of dropout can only err in one direction, viz. fish can (and do) drop out early (before they are fatigued), but not late (after they are fatigued).

These limitations, coupled with length-distributional features of the experimental populations, reduced the measurable differences and obscured the

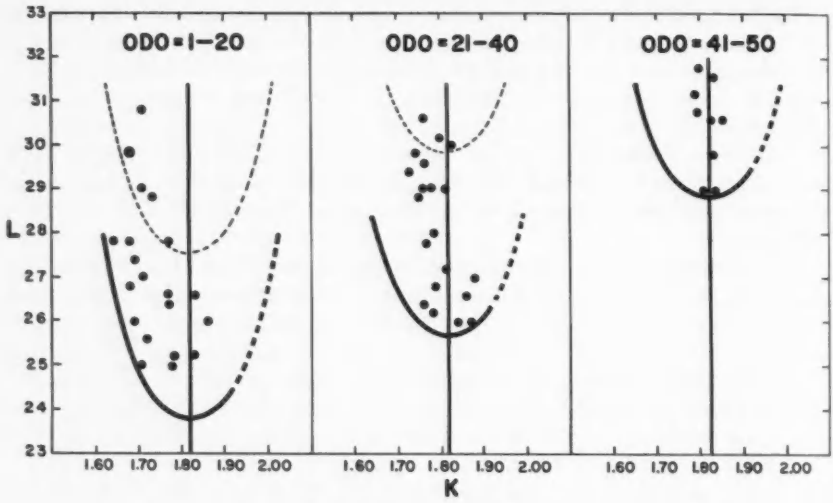

FIG. 4. Scatter diagrams relating condition (K) to length (L) at three successive levels of performance (ODO-groups 1–20, 21–40, 41–50) in test 29.

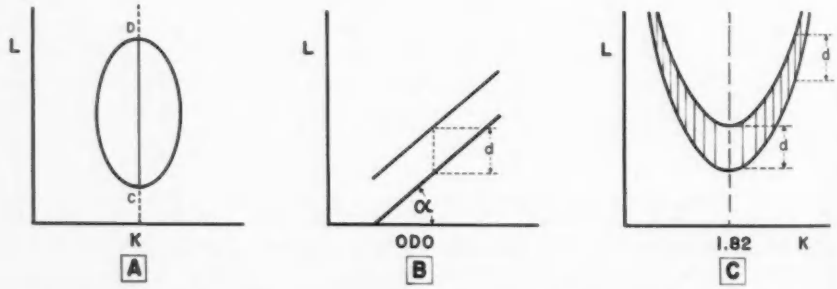

FIG. 5. Three relationships pertaining to performance: A, between length (L) and condition (K) in large random samples of fry migrants; B, between length (L) and performance (ODO) of fish in similar condition; slope is determined by α; C, between length (L) and condition (K) of those individuals within a large sample that show similar performance; d,variation width of rheotactic threshold response.

exact relationship. Only a few subsamples of a sufficiently narrow length range were available because of too limited sample sizes. In these cases a usually significant ($p \leq .05$) difference was obtained with a nonparametric covariance technique for a subdivision into three groups: near optimum K-values, below, and above. Many significant differences were found in available combinations of only two of these three groups, usually the near optimum and below. Further subdivision was not feasible and the "exponential" character of the relationship could not be proven with the data on hand.

To show the "fit" of the surmised dome-shape to the data, Fig. 4 shows test 29 broken up into three successive periods of time (ODO) with all individuals plotted for length over condition in the appropriate time period. Especially note that for all lengths a trend in time is obvious from more extreme (low) K-values to near optimum (around 1.82). At the same time a shift occurs in the size of the fish dropping out. These two factors combined result in a boomerang-shaped area, between two limiting curved lines, that comprises, as expected, small fish in optimal condition only and, at the same time, larger fish in more extreme conditions only. In time the area shifts up through the population as an increasing effort is required. The width of band between the two lines and some points above it are effects of variation in rheotactic response threshold and of premature dropout.

The data show that the optimum condition values for Lakelse sockeye migrant fry lie between 1.80 and 1.85 on preserved fish.

As far as the remaining variation is concerned, a large variation in threshold of positive rheotactic response when tiring was evident from observation of individual fish. During a test many fish started drifting back slowly with the current before they were truly fatigued and approached the electrified screen repeatedly. Frequently this resulted in the fish "accidentally" dropping out, i.e. for reasons other than a lack of physical strength. Fish with a strong rheotactic response did not come near the electrified screen until truly fatigued. It is this variation in response threshold which I consider to be the main source of variation in this type of experiment. There was no indication that the degree of variation varied between the four subject groups studied.

The general information obtained from this experiment can be synthetized in a three dimensional graph relating length, condition, and performance of a large sample of fry migrants. It contains the three biaxial relationships shown in Fig. 5: (A) the elliptical relationship (of a scatter diagram) between length and condition as displayed by large samples taken from a natural run of fry migrants and from the production run of the hatchery; (B) the linear relationship between length and performance; and (C) the boomerang-shaped relationship between length and condition (K-factor) of fry displaying similar performance. The graph is constructed for that period in the development of a fry population where the long axis of the ellipse relating length to condition coincides with optimum condition of the fry so that fish with both higher and lower K-values than optimal are included. Actual fry populations do pass through this stage, which coincides with average time of migration. Figure 6 shows the graph with X-axis = condition, Y-axis = length, and Z-axis = performance (as order of dropout). The line AB with slope α represents the order of dropout (performance) of those fry that are in optimal condition and corresponds with line CD through the base ellipse. The variation in performance introduced by the variation in condition is given by the downward slope of the graph on each side of line AB; the "boomerang shape" in the base ellipse is traceable in the graph for one particular level of performance as illustrated. The variation in threshold response for all fish of similar length and condition

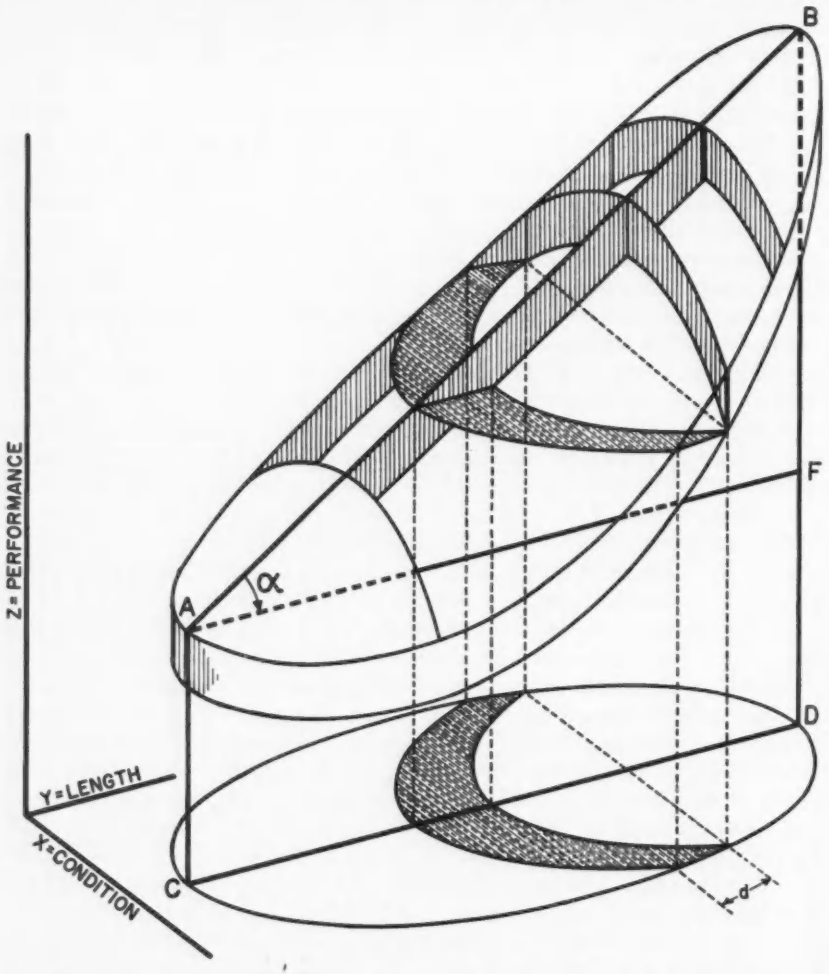

FIG. 6. Relationship between length, condition, and performance (as ODO) of a large population of fry migrants, at the time most fry are in optimal condition. This graph is based on the three biaxial relationships shown in Fig. 5.

is given by the "thickness" of the graph, which can also be traced to the base ellipse, where it is represented in the width (d) of the "boomerang" shape.

B. PREDATION TESTS

MATERIALS AND METHODS

The main objective of this experiment was presented in the Introduction. Each test was executed by simultaneously offering two groups of fry, differentially marked by the removal of one ventral fin, to a group of predators in a

glass aquarium. The aquaria used measured 92×48×46(H) cm, containing approximately 180 liters (the first six tests), and 62×32×31(H) cm, containing approximately 55 liters (all other tests). The tanks were devoid of any structures giving possible visual protection to the fry. A continuous exchange of water was maintained in all tanks, and all tests were run under favourable, ambient conditions of temperature, oxygen level, etc., as determined by the hatchery water supply.

Two groups of predators, all immature cutthroat trout, were used, one group consisting of two fish with a combined weight of 150 g and the other group of three smaller fish with a combined weight of 130 g. All five fish were obtained from the Lakelse River.

After introduction of the fry the predators were allowed to remove approximately 50% of them; the remainder was then removed and preserved in 5% formaldehyde solution for later analysis. Tests in which only 20 or less fry were left at termination were omitted. The reason for these limits is given below. Surviving fry were never used in a second trial to avoid effects of learning. There was no evidence of learning in the predators in regard to selectivity.

Analysis of the Data

Under the limiting conditions of the experimental procedure, differential predation is still controlled by a number of factors. Some of these (the first three as given below) are the basic parameters of a differential predation situation because they are immediate effects of the causal mechanisms, and are thus of great importance biologically. The others are of a secondary nature as they only modify the effects originated by the primary factors, and are thus largely of statistical importance.

1. *Discovery rate.* — A difference in discovery rates between two groups of simultaneously available fry would constitute a basis for differential predation. This factor could be of considerable importance under natural conditions, but is considered inconsequential in this experiment because the fry from different incubational sources mingled freely and were fully and equally exposed to the predators at all times.

2. *Attack rate.* — After discovery the predator may attack the two groups at different rates, i.e. exert an active selection by rejecting or accepting each prey on the basis of a certain characteristic (or number of characteristics) that is perceived by the predator and influences his attack behaviour. This parameter is of great importance but could not be established in this experiment because the individual fish could not as a rule, be identified to source while in the tanks.

3. *Capture rate.* — After attack is initiated a difference may occur in the rates of capture for the two groups. The predator is, again, instrumental in effecting the selection but in this case it is a *passive selection* because the selective mechanism is not situated with the predator but with the prey, i.e. some characteristic (or number of characteristics) of the prey, such as a superior avoidance reaction, affects the capture-to-attack ratio directly. As with the

attack rate, this basic parameter could not be established directly in these tests and for the same reason. Therefore, the statistic to express vulnerability to predation must derive from the overall predation rate, which is a confounded parameter.

4, 5. *Availability* and *Level of predation.* — If at the onset of a test different numbers are available in each group of prey and both groups are subject to predation, the actual numbers eaten will reflect the original ratio in which both groups were available. By relating the numbers eaten to the numbers available no such dependency occurs, therefore the statistic used must derive from predation *rates*.

A different problem occurs when the availability ratio changes during a test: the preferred group decreases in relative abundance and increasingly fewer individuals will be taken relative to the number taken from the other group. Therefore the measured predation rate of the *preferred* group, which must be based on the overall results of a test, is lower than the *actual* instantaneous rate for that group, and increasingly so as the level of predation increases (within each test). The same phenomenon occurs, between tests and at comparable levels of predation, in those cases where the difference in predation rates between the two groups increases. A correction for this bias is not easily made and was considered unnecessary and therefore not carried out. However, to keep the variation in availability ratios between tests within reasonable limits and the predation rates comparable, limits were applied to the overall level of predation achieved in each test (see Analysis of the Data).

As suggested by W. E. Ricker (personal communication) a workable statistic to express the difference in predation rates is the ratio $d_P = \frac{i_1}{i_2}$, where i_1 is the instantaneous mortality (predation) rate of the first group, as listed in the tables, and i_2 that of the second group. It was described and used by Parker et al. (1963) and before them by Ricker (1949).

The observed differences in predation rates were tested for significance with the χ^2-method. The results are shown in the tables.

Tables VIII–XII relate all pertinent information. Each table refers to one series of comparable tests on the same sources of fry. In very few of the individual tests are differences between groups significant, but consistent results within each series, with the possible exception of series P-4, allow pooling the data, which, in effect, increases the sample size and results in probability levels of less than 0.05 for the three main test series, P-1 through P-3. The consistency of the results within each series is confirmed with a test of heterogeneity using the difference between the χ^2 values obtained on the pooled data and the unbiased summed χ^2 values of the individual tests. The results of these tests and the significance levels are also shown in the tables.

Results

The results are grouped in series by source of test material.

P-1. *"Hatchery" fry versus "wild" fry.*— Six tests were run on fry of these two sources (Table IX). All showed similar results favouring the wild

TABLE IX. P-1. Predation on "hatchery" and "wild" fry. Start = number of fry in each group at start of test. Observed = number of fry in each group left at termination of test. Expected = number of fry in each group expected under H_0 (no differential mortality). p = probability of observed frequency occurring under H_0; s = survival rate; i = instantaneous mortality rate, $s = e^{-i}$; d_P = ratio of instantaneous mortality rates, i_1/i_2.

	Start		Observed		Expected					s		i		
Test	Hatchery	Wild	Hatchery	Wild	Hatchery	Wild	χ^2	df	p	Hatchery	Wild	Hatchery	Wild	d_P
1	50	50	25	34	29.5	29.5	1.38	1	$.3 > p > .2$	0.50	0.68	0.693	0.386	1.80
2	25	75	13	46	14.75	44.25	0.28	1	$.7 > p > .5$	0.52	0.61	0.653	0.494	1.32
4	25	75	6	26	8	24	0.66	1	$.5 > p > .3$	0.24	0.35	1.427	1.050	1.36
5	50	50	13	23	18	18	2.77	1	$p = .1$	0.26	0.46	1.347	0.776	1.74
6	25	75	7	30	9.25	27.75	0.73	1	$.5 > p > .3$	0.28	0.40	1.273	0.916	1.39
10	50	50	17	20	18.5	18.5	0.24	1	$.7 > p > .5$	0.34	0.40	1.079	0.916	1.18
Σ	225	375	81	179	98	162	4.63	1	$p = .033$	0.36	0.48	1.022	0.734	1.40

Test for heterogeneity: $\Sigma\chi^2$ 6.06
Difference 1.43 $p = .92$

fry over the hatchery fry d_P being 1.40 for the summed data ($p = 0.033$). The tests showed little heterogeneity ($p = 0.919$).

P-2. *"Basket" fry versus "gravel" fry.*— Seven tests were run on fry of these sources (Table X). All tests but one were run on approximately 100 fry; the exception, test 30, on double that number. Because this test was allowed to continue until the number of fish remaining was similar to those of the other tests, a much higher percentage of the original number was removed, about 75% in comparison with about 50%; hence, the greater change in availability could render the results incomparable with those of the other six tests. However, as can be seen from the two rows in Table X that show the results for the summed data excluding and including test 30, the difference in outcome is negligible. The overall results indicate a difference in vulnerability ($d_P = 1.39$) virtually identical to that between hatchery and wild fry and favouring the gravel fry over the basket fry. The degree of heterogeneity was low ($p = 0.92$).

P-3. *"Basket" fry versus "wild" fry.*— Seven tests were run on fry of these sources (Table XI). A consistently superior response was evident in the wild fry, d_p being 1.80 for the summed data ($p < 0.001$). The degree of heterogeneity was sufficiently low ($p = 0.7$).

P-4. *"Hatchery" unfed fry versus "hatchery" fed fry.*— In this series (Table XII) two groups of fry were used from the same source, obtained on 2 successive days, but one group was fed a mixed diet of meat, liver, shrimp, and pelleted food for about 2 weeks, and the second group, which was held under similar conditions, was not fed. The overall results ($d_P = 1.35$) indicate a difference in response between these groups resembling that between "hatchery" and "wild," and between "basket" and "gravel" fish.

The two groups were tested when significant differences in body length and weight had developed. A sample of 19 unfed and 18 fed fry showed considerable overlap in length (ranges were 25.0–28.8 mm and 27.0–31.0 mm respectively) with a difference between the means of 2.06 mm, but no overlap in weight (ranges of 104–168 mg and 169–262 mg) with a difference between the means of 72.1 mg.

The outcome of test 8 with a d_P of 0.97 was unexpected and, in the light of all other findings, erratic, but the test cannot be disqualified as all known experimental conditions including fish sizes and conditions were in order. It may be an effect of chance.

P-5. *"Hatchery" fry in good condition versus "wild" fry in poor condition.*— Two more tests were run on fish differing in length and condition, but in this case both were unfed and obtained from different sources (Table XIII). One group consisted of wild fry of an early release date which were held until they had no yolk left and were becoming emaciated. The hatchery fry released themselves 3 days previous to the testing date and appeared in excellent condition and had some yolk left. The two groups performed nearly identically, which indicates that the advantage the wild fry exhibited earlier was negated by their presently poorer condition. No factors other than length and condition

TABLE X. P-2. Predation on "basket" and "gravel" fry. For explanation of symbols see Table IX.

	Start		Observed		Expected					s		i		
Test	Basket	Gravel	Basket	Gravel	Basket	Gravel	χ^2	df	p	Basket	Gravel	Basket	Gravel	d_P
15	50	50	20	30	25	25	2.00	1	$.2 > p > .1$	0.40	0.60	0.916	0.511	1.79
17	50	36	30	24	31.4	22.6	0.15	1	$p = .7$	0.60	0.67	0.511	0.400	1.28
18	49	47	18	19	18.9	18.1	0.088	1	$.8 > p > .7$	0.37	0.41	0.994	0.892	1.11
19	50	50	20	24	22	22	0.36	1	$.7 > p > .5$	0.40	0.48	0.916	0.734	1.25
20	50	50	17	27	22	22	2.27	1	$.2 > p > .1$	0.34	0.54	1.079	0.616	1.75
29	50	50	24	31	27.5	27.5	0.89	1	$.5 > p > .3$	0.48	0.62	0.734	0.478	1.53
Σ(15–29)	299	283	129	155	146.8	137.2	4.47	1	$p > .038$	0.43	0.55	0.840	0.598	1.40
30	100	100	19	32	25.5	25.5	3.31	1	$.1 > p > .05$	0.19	0.32	1.660	1.139	1.46
Σ(15–30)	399	383	148	187	172.3	162.7	7.06	1	$p = .009$	0.37	0.49	0.994	0.713	1.39
					Test for heterogeneity:	$\Sigma\chi^2$	9.068	7						
						Difference	2.01	6	$p = .92$					

TABLE XI. P-3. Predation on "basket" and "wild" fry. For explanation of symbols see Table IX.

	Start		Observed		Expected					s		i		
Test	Basket	Wild	Basket	Wild	Basket	Wild	χ^2	df	p	Basket	Wild	Basket	Wild	d_P
21	50	50	18	36	27	27	6.00	1	$.02 > p > .01$	0.36	0.72	1.022	0.328	3.12
22	50	50	10	14	12	12	0.66	1	$.5 > p > .3$	0.20	0.28	1.610	1.273	1.26
23	50	50	11	31	21	21	9.53	1	$.01 > p > .001$	0.22	0.62	1.514	0.478	3.17
24	50	50	19	28	23.5	23.5	1.76	1	$.2 > p > .1$	0.38	0.56	0.968	0.580	1.67
26	50	50	19	25	22	22	0.82	1	$.5 > p > .3$	0.38	0.50	0.968	0.693	1.40
27	50	50	22	31	26.5	26.5	1.53	1	$.3 > p > .2$	0.44	0.62	0.821	0.478	1.72
28	50	50	20	28	24	24	1.33	1	$.3 > p > .2$	0.40	0.56	0.916	0.580	1.58
Σ	350	350	119	193	156	156	17.55	1	$p < .001$	0.34	0.55	1.079	0.598	1.80
						Test for heterogeneity: $\Sigma\chi^2$	21.63	7						
						Difference	4.08	6	$p = .67$					

TABLE XII. P-4. Predation on unfed and fed "hatchery" fry. For explanation of symbols see Table IX.

	Start		Observed		Expected		Difference				s		i		
Test	Unfed	Fed	Unfed	Fed	Unfed	Fed	Unfed	Fed	χ^2	p	Unfed	Fed	Unfed	Fed	d_P
7	50	50	20	25	22.5	22.5	+2.5	−2.5	0.556	$.5 > p > .3$	0.40	0.50	0.916	0.693	1.32
8	50	50	19	18	18.5	18.5	−0.5	+0.5	0.027	$.9 > p > .8$	0.38	0.36	0.968	1.022	0.97
9	48	52	11	26	17.76	19.24	+6.76	−6.76	4.94	$.05 > p > .02$	0.23	0.50	1.470	0.693	2.12
Σ	148	152	50	69	58.76	60.24	+8.76	−8.76	2.28	$p = .138$	0.34	0.45	1.079	0.798	1.35

TABLE XIII. P-5. Predation on "hatchery" fry (H) in good condition and "wild" fry (W) in poor condition. For explanation of symbols see Table IX.

	Start		Observed		Observed		Difference				s		i		
Test	H	W	H	W	H	W	H	W	χ^2	p	H	W	H	W	d_p
13	50	50	25	23	24	24	−1	+1	0.083	$.8 > p > .7$	0.50	0.46	0.693	0.776	0.89
14	75	25	42	14	42	14	0	0	0	$p = 1.0$	0.56	0.56	0.580	0.580	1.00
Σ	125	75	67	37	66	38	−1	+1	0.043	$p = .747$	0.536	0.493	0.624	0.707	0.88

of the fish were known to differ between the two groups. Mean lengths determined from samples of these stocks were approximately 26.1 mm for the hatchery stock and 29.2 mm for the wild; weights are not available.

Discussion

The results of all predator tests on unfed fish of normal, good condition can be combined into a series of decreasing degree of vulnerability to predation by relating to each other the ratios between various groups as obtained by experiment (P-1 through P-3). We obtain, by calculation, the following series: basket > hatchery, $d_P = 1.28$; hatchery > gravel, $d_P = 1.10$; and gravel > wild, $d_P = 1.28$. Superimposed on this, as demonstrated by series P-5, is the effect of condition of the fish, which can nullify the original advantage the better performing groups have over the lower.

Mechanism of Selective Predation

Having established differences in predation rates on the four groups of fry, it is of paramount importance to establish the mechanism by which these differences come about. From the point of view of artificial propagation, knowledge of this mechanism is essential if it pinpoints the very characteristics of the fry responsible for the differences, so that cultivation methods can be sought to optimize those characteristics that reduce vulnerability to predation and/or alternatively to minimize those that increase vulnerability.

For a proper understanding of this mechanism we ought to know the respective effectiveness of active and passive selection by the predator and the characteristic, or set of characteristics, of the prey that governs the effective mode, or modes, of selection. As previously explained, no direct measurement was possible of the individual values of these modes, but some additional information regarding the selection mechanism and the fry characteristics involved can be deduced from the results.

A first possibility, as brought forward by Parker et al. (1963), to explain experimentally established differences in vulnerability to predation between fin-clipped and unmutilated pink fry, is that the predator can visually, or otherwise, recognize individuals of two admixed experimental groups as being different. The same mechanism may apply to recognizable source-induced differences between the four groups studied. A further assumption however is required to explain why the predator would prefer to attack one group over the other. Parker assumes that the marked fish stand out from the rest of the school by being recognizably different and thus lose the statistical protection presumably afforded by the school, but only if one group forms a decided minority amongst many others can this mechanism explain which group will be preferred: fish of the minority group are likely to be more conspicuous and hence easier to single out than fish of the majority group. This condition was achieved in Parker's experiment where the marked and unmarked fry were consistently supplied in the ratio of 1:3. If this argument holds and no other factors are of effect, a reversal of this ratio should result in a reversed preference of the same magnitude.

If the two groups are supplied in equal numbers, however, as was the case in most of our tests, either no preference should take place or it should vary randomly between tests if the predator executes "runs" of a particular but random choice. Our results show a consistent preference for one group in each test of the main series P-1 through P-3, which proves that some other factor must be present that is independent of distribution.

Active selection then would require an instinctive or learnt knowledge by the predator of differences between groups, coupled with an instinctive or learnt preference for the "abnormal." The possibility of an innately known "normal" (= wild) fry is considerably weakened by the fact that a consistent selection also took place in those tests where "normal" fry were not used (series P-2). The possibility of a learnt knowledge of what constitutes a "normal" or "abnormal" fry requires further assumptions and this possibility becomes remote if we consider the rather small differences in predation rates, and other differences between the groups.

As a last possibility an entirely different mechanism may be envisaged that does not require any "absolute" knowledge about the fry. It requires that the predator compares individual prey that are simultaneously available (school) and each time selects on a relative basis, e.g. for the smaller sized fish within the range available, regardless of absolute size. Under the conditions of this experiment active selection by relative size alone would explain the differential predation rates as found.

An attractive alternative explanation is available, however, that does not require an active choice by the predator, but attributes the differential predation rates directly to the fry, i.e. to some characteristic of the fry that influences the capture-to-attack ratio. If we compare the differences in predation rates for the four subject groups with the differences in swimming performance for these same groups as related earlier, an excellent agreement is evident: the two sets of differences agree both in direction and in order of magnitude (Fig. 7); and a causal relationship between the results of the two experiments is likely. As was demonstrated above, the key factor determining the differences in swimming performance was the size of the fish. Methods similar to those used to establish the extent of agreement between length and swimming performance could not be employed with the predation tests. The agreement between the two experiments is so close, however, that it appears reasonable to expect a similar direct relationship, and the conclusion is warranted that for fish of similar condition the differences in size account, at least, to a great extent for the observed differences in both swimming performance and vulnerability to predation. It is not clear whether the size difference is the indirect cause of selective predation acting through an active choice by the predator, or whether it acts directly through differences in swimming performance affecting the capture-to-attack ratio. I consider the latter mechanism as the more plausible of the two possibilities.

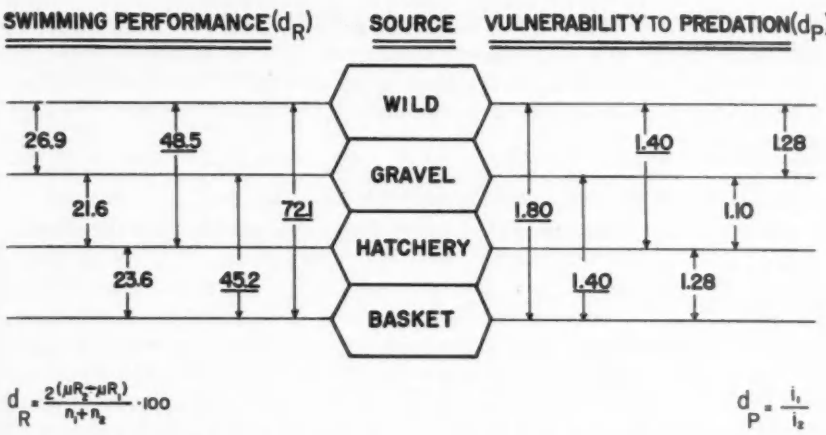

FIG. 7. Diagram illustration the differences in swimming performance and in vulnerability to predation as established for four groups of unfed migrant sockeye fry differing in incubational treatment only. Emperical values are underlined; deduced values are not underlined.

RESTRICTED SCOPE OF THE EXPERIMENT

Size differences do not necessarily account for the full extent of the measured differences in vulnerability; source-induced differences other than length may also affect, albeit to a much lesser degree, the predator–prey relationship. Further tests with selected groups of fry would be required to investigate this possibility. It is most unlikely, however, that the relationship between length and vulnerability would be seriously affected. Also, the experiment reported here was purposely biased in favour of the effect of swimming performance on vulnerability to predation. In a less limiting environment (space and cover!) further differences in vulnerability between groups may occur as a result of factors entirely unrelated to swimming performance, e.g. behavioural differences that affect the discovery rate.

The work reported here is not an exhaustive study of all effects resulting from various methods of incubation; it is limited to those factors that strongly affect swimming performance as measured directly in a simple swimming test, and indirectly in a more complex predation test. Within these limits, however, it has served to establish the great importance of one factor known to be affected by incubation techniques: length of fry-migrants is a key factor in their survival potential.

SENSITIVITY OF THE TWO TESTING METHODS

The predator test is far less sensitive than the swimming performance test, i.e. for the same sample size the probability that the difference established between any two groups of fry is not due to chance is much lower in the predator test than in the swimming performance test. This probably indicates a real decrease in the effectiveness of the differences in size on the differences in

response in the predator tests, which is hardly surprising if we consider the difference in the two methods of stimulation. The swimming performance test, therefore, appears to be the more useful method of obtaining a general measure of performance and is better suited for routine "quality" testing of fish stocks.

Implications of Results to Propagation Techniques

From the viewpoint of artificial propagation we can consider the diagram (Fig. 7) as a comparative quality table. We deduce from it that the technique employed at the Scully Creek Hatchery that used gravel during the advanced premigrant stage (producing the "hatchery" fry) constituted an improvement, in terms of performance, over the technique of incubating the brood in hatchery baskets up to the migrant stage (producing the "basket" fry). An experimental technique utilizing gravel during the alevin and premigrant stages (producing the "gravel" fry) was again an improvement in terms of performance of about equal magnitude, but it appears that this technique is still one step of similar size removed from naturally propagated stock (the "wild" fry). There are reasons to believe that this last gap can also be closed, at least to a certain extent, largely by changes in engineering.

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A System to Digitize Bathythermograph Aperture Cards[1]

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ABSTRACT

This paper describes a system which allows the automatic transformation of bathythermograph (BT) data to their digital equivalent. The BT data now stored on aperture cards, a technique described by Sauer (J. Fish. Res. Bd. Canada, **21**(3), 1964), form the input to digitization equipment especially modified for this application. A description of the system and required equipment is followed by the mathematical approach employed in the Cartesian to BT grid coordinate transformation. It comprises a type of double inverse interpolation in the coordinates of the major grid intersections. Firstly, a point P on the BT trace is localized in or near a group of four "cells" in the grid. Secondly, the grid data belonging to this four-cell block are used in an iterative process based on two separate Lagrangian interpolations. The latter, both 3-point formulae, appear more than adequate in coping with BT grid distortions. This, in turn, leads to a two-dimensional fit up to fourth order terms. Any subsequent needs for translation, rotation, and linear amplification or reduction of the BT trace relative to its grid may be dealt with by means of a linear transformation.

INTRODUCTION

More data have been accumulated on temperature than on any other variable feature in the upper layers of the world ocean. This is primarily due to the introduction of the bathythermograph (BT), first introduced by Rossby and Montgomery (1935) and further developed by Spilhaus (1938). The bathythermograph is employed by nearly all oceanographic laboratories and navies throughout the world.

It comprises a rugged, low accuracy device of good precision that produces a continuous record of water temperature versus depth. The instrument records the data on 1 × 1.75-inch smoked or gold-plated glass slides referred to as bathythermograms. In recent years there has been a sharp increase in the collection of BT data, primarily as a result of the greater effort in worldwide oceanographic research and a stepped-up vigilance in anti-submarine warfare. As a result, the enormous amount of BT data thus accumulated is now creating serious problems in the processing and evaluating stages. The expendable BT (XBT), a device introduced by Francis and Campbell (1965), is rapidly growing in popularity and in doing so, it also adds its measure to the volume of data to be processed.

This situation showed signs of improvement when both Canada and Great Britain switched to a technique whereby the grid/slide combination is

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transferred to an aperture card. In Canada, this is achieved in a one-step operation by means of the BT Processor (Fig. 1), a modification by Bowler and Forward (1964) of the 3M Processor Camera.

In addition to the obvious advantages of preserving the original analog trace for detailed analyses of thermal structures, there exists an immediate need for the storage of BT data in digital form. This would allow rapid machine analysis of broadly defined thermal structures in the upper layers. In this regard, a number of objective methods for isolating oceanographic phenomena have been suggested by Boston (1966).

A system that permits the low-cost, efficient means of BT digitization forms the subject of this paper.

SYSTEM

After a prolonged search, the authors located two low-cost devices, capable of simple interfacing, that would yield the desired result, namely the

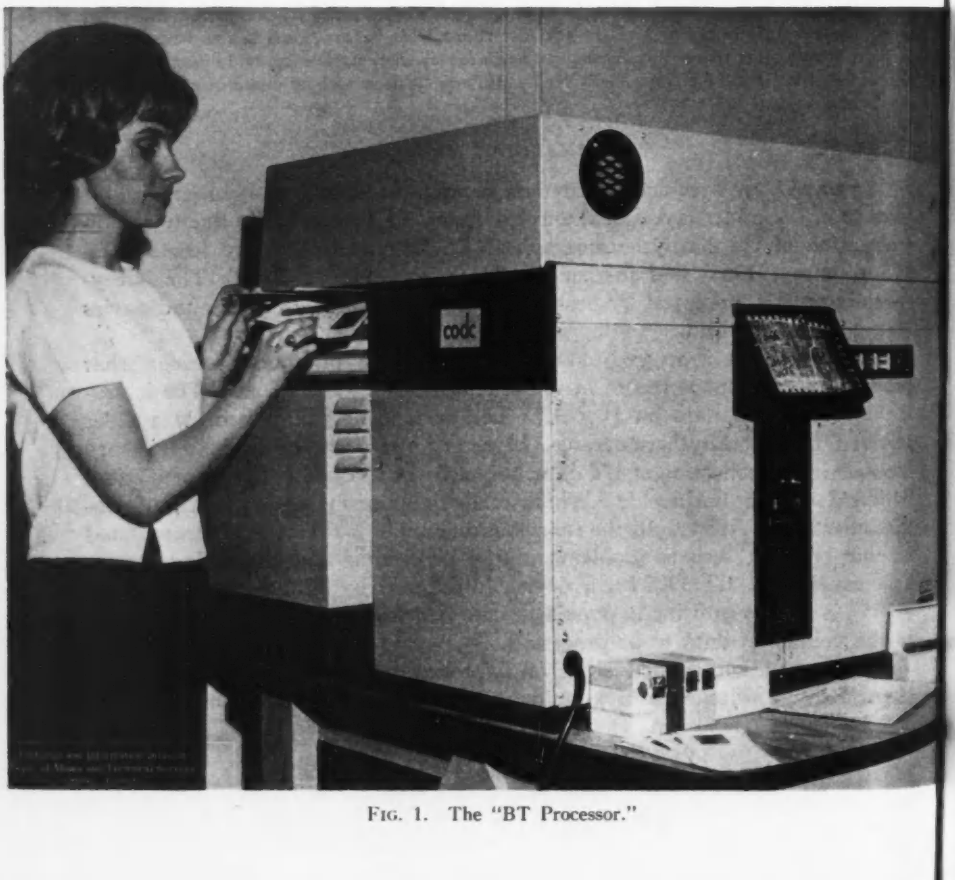

FIG. 1. The "BT Processor."

semiautomatic digitization of BT aperture cards. The combined hardware, hereafter referred to as the "BT Digitizer" (Fig. 2), comprises a Caps-Jeffree projector with the automatic aperture card feed feature and a D-MAC curve follower unit. They are interfaced to work in unison.

The cards are fed from a hopper by depressing a button positioned at the front of the digitizer. This results in the projection of the BT image portion of the aperture card on to the digitizer table. A specialized curve follower is employed which eliminates any distortion that might be introduced when projecting an image from an overhead position. The output mode selected is minimum X-incremental. The X–Y output stored on magnetic tape is supplemented by activating the keyboard to provide specific control information.

Emphasis has been placed on operator ease and most of the decision-making burden is carried by the computer. The remainder is described in an operator manual to ensure standardized procedures. The time to complete one record is approximately 45 sec depending on the complexity of the trace.

The flow diagram depicted in Fig. 3 illustrates the method adopted by the Canadian Oceanographic Data Centre. The digitizer output combined with its corresponding reference information and previously created grid file serve as input to the computer. The computer in turn makes the required coordinate transformations and carries out any necessary translation, rotation, and linear reduction of the trace relative to its grid.

In deciding upon the digitization interval for stored BT data in the Canadian Oceanographic Data Centre, the authors were guided by the following deliberations.

The bathythermograph was primarily designed to measure changes of temperatures with changes in depths. Bralove and Williams (1952) stress the importance of the measurement of *changes* in view of the fact that the *values* of temperature and depth registered by the bathythermograph are arbitrarily established by superimposed grids and correction factors.

The "rated" reproducibility as well as its accuracy to measure changes of temperature with depth are assumed to be ± 0.1 F degree and $\pm 1\%$ of the full depth range.

However, carefully conducted tests and evaluations such as those reported by Stewart (1963) reveal that under routine operating conditions the rated temperature precision cannot be achieved. In practice, a precision of ± 0.4 F degree for temperature and $\pm 1\%$ of full range for depth is more acceptable.

Bearing in mind the above limitations, the Canadian Oceanographic Data Centre reduces the digitized computer output by storing the depth coordinates to the nearest whole metre at uniform temperature intervals of 0.1 C degree, or approximately half the measurement precision of the instrument.

METHOD

1. No assumptions are made about either the equations of the grid lines or local linearities of the latter.

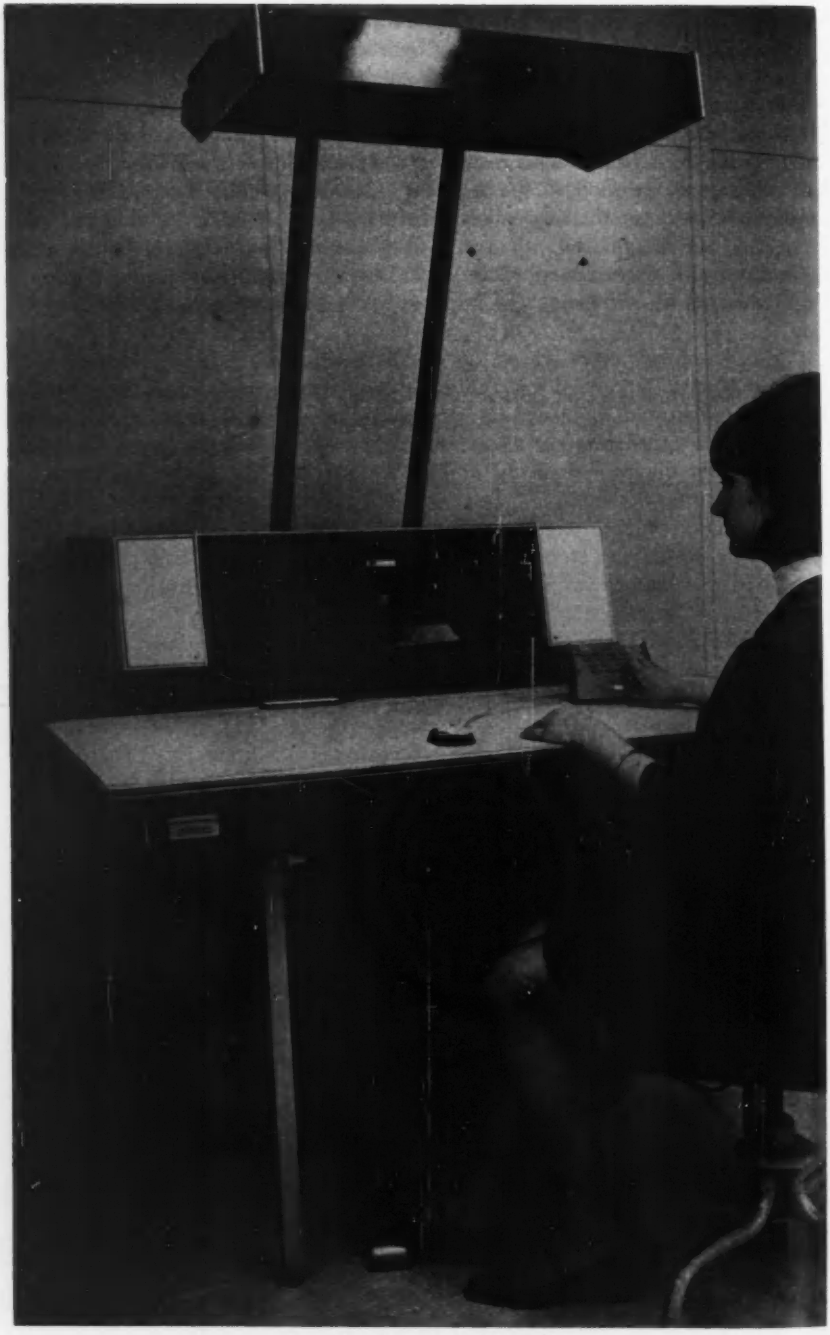

FIG. 2. The "BT Digitizer."

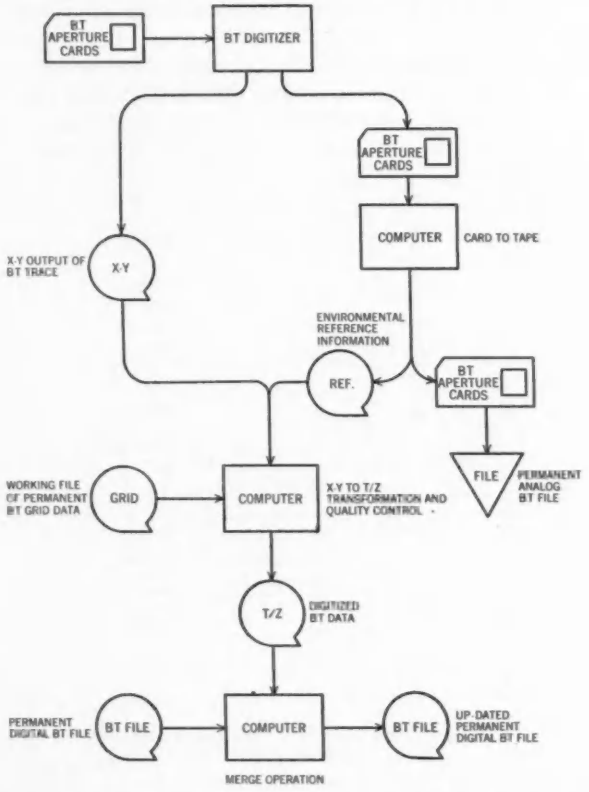

FIG. 3. Schematic flow diagram of the BT digitization system.

2. Grid data are recorded in the following way: since the grid lines are curves of constant T and constant z, numerically separated by constant increments h_T, h_z, respectively, we refer to the grid point (i, j) having coordinates $T = T_0 + ih_T$ and $z = z_0 + jh_z$, where i, j are integers in the ranges $0 \leqslant i \leqslant M$, $0 \leqslant j \leqslant N$ (see Fig. 4). Two matrices $\underline{X}$ and $\underline{Y}$ are recorded on file whose elements are the Cartesian coordinates of the grid intersections with respect to the axes of the digitizer table, thus $\underline{X}_{ij} = x_{ij}$, $\underline{Y}_{ij} = y_{ij}$ where(x_{ij}, y_{ij}) is the point with:

$$T = T_i = T_0 + ih_T$$
$$z = z_j = z_0 + jh_z$$

3. Given the Cartesian coordinates (x_p, y_p) of a point P lying wholly within the grid boundary, the 1:1 corresponding (T,z) coordinates are found in the following way:

4. First a grid point (i,j) nearest P is determined by a systematic sweep over the values $d_{ij}^2 = (x_p - x_{ij})^2 + (y_p - y_{ij})^2$. If P is such that more than one set (i,j) satisfies the minimum requirement on d_{ij}^2, i.e. is such as to be equidistant from two or more grid points, then that pair (i,j) is taken which has the lowest value of: $i + 1 + (j + 1)^2$. Since the computer must have some criterion to decide upon, and since with either 2, 3, or 4 of the possible pairs of type (l,k), $(l+1,k)$, $(l,k+1)$, $(l+1,k+1)$ which might occur in combination, the quantity $i + 1 + (j + 1)^2$ always has a unique minimum for non-negative integer i and j.

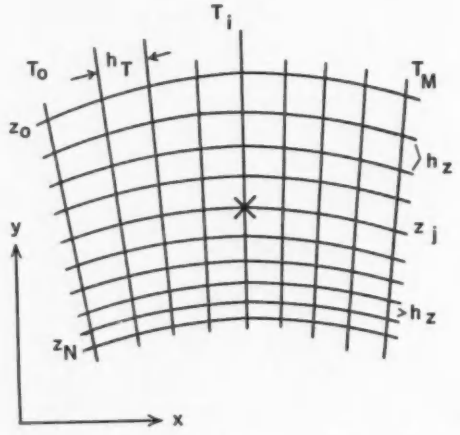

FIG. 4. Generalized BT grid with digitizer table axes x, y.

5. P is now definitely located within a block of four "cells" (see Fig. 5) as follows: if the nearest neighbour (i,j) selected in step 4 is not a boundary point of the grid mesh, then the four-cell block is described by mesh points (l,k) where $(i-1) \leqslant l \leqslant (i+1)$ and $(j-1) \leqslant k \leqslant (j+1)$. If the nearest neighbour (i,j) has either or both (a) $i=0$ or M, (b) $j=0$ or N, we use the block determined by mesh points (l,k) where: $(|i-1|-1) \leqslant l \leqslant (|i-1|+1)$ and $(|j-1|-1) \leqslant k \leqslant (|j-1|+1)$, modifying the range of l and/or k according as conditions (a) and/or (b) occur.
6. The nine mesh points involved in the four-cell block constructed in step 5 are used in a type of double inverse interpolation to find the T_p,z_p corresponding to the given x_p,y_p. Two 3×3 submatrices are extracted from $\underline{X}$ and $\underline{Y}$ giving, respectively, the x and y coordinates of the nine points forming the cell block and are shown in Table I.
7. Ideally we wish to find $T_p = T_i + i_p h_T$ and $z_p = z_j + j_p h_z$ such that when T_p,z_p are used in a double forward interpolation involving the data of the entire grid then the values x_p,y_p are exactly reproduced. This is the best that can be done, and would be rather complicated, but provided

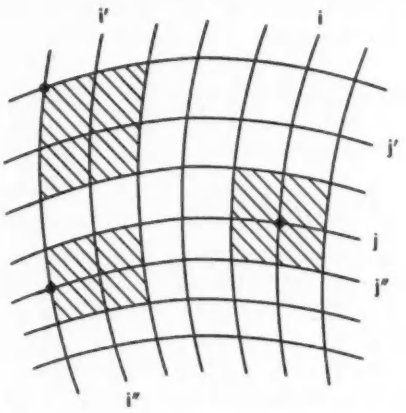

FIG. 5. Three four-cell blocks (shaded) and their corresponding nearest neighbour mesh points (●) within a grid system depicting exaggerated distortion.

TABLE I.

	X submatrix			Y submatrix		
Row j–1	$x_{i-1,j-1}$	$x_{i,j-1}$	$x_{i+1,j-1}$	$y_{i-1,j-1}$	$y_{i,j-1}$	$y_{i+1,j-1}$
Row j	$x_{i-1,j}$	$x_{i,j}$	$x_{i+1,j}$	$y_{i-1,j}$	$y_{i,j}$	$y_{i+1,j}$
Row j+1	$x_{i-1,j+1}$	$x_{i,j+1}$	$x_{i+1,j+1}$	$y_{i-1,j+1}$	$y_{i,j+1}$	$y_{i+1,j+1}$

nonlinearities are not too severe a suitable approximation can be made using only the information in Table I. Firstly, a Lagrangian interpolation (Kopal, 1961) in rows j–1, j, and j+1, respectively, of the X submatrix in Table I would yield, if T_p were known, the three values x_k^p of the x coordinate at the intersection of the BT curve $T = T_p$ with BT curve $z = z_k$, where:

$$x_k^p = x_{i-1,k}\left[\frac{(T_p-T_i)\,(T_p-T_{i+1})}{2h_T^2}\right] + x_{i,k}\left[\frac{(T_{i-1}-T_p)\,(T_p-T_{i+1})}{h_T^2}\right] + x_{i+1,k}\left[\frac{(T_p-T_{i-1})\,(T_p-T_i)}{2h_T^2}\right]$$

for $k = j-1, j, j+1$. Similarly an interpolation of Lagrangian type among the x_k^p using z_p, if the latter were known, would give:

$$x_p = x_{j-1}^p \left[\frac{(z_p-z_j)\,(z_p-z_{j+1})}{2h_z^2}\right] + x_j^p \left[\frac{(z_{j-1}-z_p)\,(z_p-z_{j+1})}{h_z^2}\right] + x_{j+1}^p \left[\frac{(z_p-z_{j-1})\,(z_p-z_j)}{2h_z^2}\right]$$

An analogous process with the elements of submatrix $\underline{Y}$ in Table I would give y_p. The method which follows uses the given coordinates x_p, y_p in order to determine T_p, z_p. The x_k^p can be arranged explicitly as quadratics in T_p, therefore x_p can be written:

$x_p = A_0 + A_1T_p + A_2z_p + A_3T_p^2 + A_4T_pz_p + A_5z_p^2 + A_6T_p^2z_p + A_7T_pz_p^2 + A_8T_p^2z_p^2$ where the coefficients A_r depend only on the grid data. If we now write $T_p = T_i + i_ph_T$, $z_p = z_j + j_ph_z$, where by reason of the fact that P is confined within a four-cell block, $-1 \leqslant i_p \leqslant 1$ and $-1 \leqslant j_p \leqslant 1$, x_p can also be written:

$x_p = C_0 + C_1i_p + C_2j_p + C_3i_p^2 + C_4i_pj_p + C_5j_p^2 + C_6i_p^2j_p + C_7i_pj_p^2 + C_8i_p^2j_p^2$.

The coefficients C_r are determined by using all integer combinations of i_p, j_p and equating the left hand side of the expression to the corresponding entry in the $\underline{X}$ submatrix in Table I. This yields:

$C_0 = x_{i,j}$, $C_1 = \frac{1}{2}(x_{i+1,j}-x_{i-1,j})$, $C_2 = \frac{1}{2}(x_{i,j+1}-x_{i,j-1})$, $C_3 = \frac{1}{2}(x_{i+1,j}-2x_{i,j}+x_{i-1,j})$, $C_5 = \frac{1}{2}(x_{i,j+1}-2x_{i,j}+x_{i,j-1})$

while the remaining four coefficients are most compactly stated as matrices in which the centre element refers to grid point i,j and where the value of each element is the multiple of the corresponding entry in the $\underline{X}$ submatrix in Table I:

$$C_4 = \tfrac{1}{4}\cdot\begin{bmatrix} 1 & 0 & -1 \\ 0 & 0 & 0 \\ -1 & 0 & 1 \end{bmatrix} \quad C_6 = \tfrac{1}{4}\cdot\begin{bmatrix} -1 & 2 & -1 \\ 0 & 0 & 0 \\ 1 & -2 & 1 \end{bmatrix} \quad C_7 = \tfrac{1}{4}\cdot\begin{bmatrix} -1 & 0 & 1 \\ 2 & 0 & -2 \\ -1 & 0 & 1 \end{bmatrix} \quad C_8 = \tfrac{1}{4}\cdot\begin{bmatrix} 1 & -2 & 1 \\ -2 & 4 & -2 \\ 1 & -2 & 1 \end{bmatrix}$$

Similarly $y_p = D_0 + D_1i_p + D_2j_p + D_3i_p^2 + \ldots + D_8i_p^2j_p^2$, where the coefficients D_r are obtained from the C_r by everywhere replacing $x_{m,n}$ by $y_{m,n}$. The two equations $x_p = f(C_r, i_p, j_p)$ and $y_p = g(D_r, i_p, j_p)$ are solved simultaneously by the standard technique of taking only linear terms in double Taylor expansions (where superscript (k) means evaluation of a quantity at stage k):

$$f^{(k)} - x_p = \left[\frac{\partial f}{\partial i_p}\right]^{(k)} \cdot \delta i_p^{(k)} + \left[\frac{\partial f}{\partial j_p}\right]^{(k)} \cdot \delta j_p^{(k)}$$

$$g^{(k)} - y_p = \left[\frac{\partial g}{\partial i_p}\right]^{(k)} \cdot \delta i_p^{(k)} + \left[\frac{\partial g}{\partial j_p}\right]^{(k)} \cdot \delta j_p^{(k)}$$

and solving for the corrections $\delta i_p^{(k)}$, $\delta j_p^{(k)}$ which then yield the next pair of values in the iteration:

$$i_p^{(k+1)} = i_p^{(k)} - \delta i_p^{(k)} \text{ and } j_p^{(k+1)} = j_p^{(k)} - \delta j_p^{(k)}.$$

The cycle is started with initial approximations:

$$i_p^{(0)} = (x_p - C_0)/C_1 \text{ and } j_p^{(0)} = (y_p - D_0)/D_2$$

and is continued until some stage s for which

$$\left[\delta i_p^{(s)}\right]^2 + \left[\delta j_p^{(s)}\right]^2 < \epsilon \text{ where } \epsilon \text{ is a preset minimum.}$$

Finally the converged values of i_p, j_p give $T_p = T_i + i_p h_T$, $z_p = z_j + j_p h_z$.

8. There need be no modification when P (x_p, y_p) lies outside the BT grid, as all the equations are general and hold equally well if i_p, j_p have modulus greater than unity, except that due to non-linearity of the grid lines a three-point Lagrangian interpolation may not be sufficient to extrapolate accurately row-wise in the submatrices of Table I if P lies very far outside. However, for BT work the grid distortion is unlikely to be pronounced enough to affect the calculations.

9. Since the grid data common to a set of BT traces are filed on a single occasion together with a code number, a subsequent BT trace having the corresponding code will in general be offset with respect to the original grid whose data are to be used in the analysis. Therefore each point P on the trace must be reduced to the original axes by a linear transform:

$$x_p' = ax_p + by_p + c,\ y_p' = dx_p + ey_p + f$$

and then x_p', y_p' are treated as already described in steps 3 through 7. A linear transformation suffices if there is only translation, rotation, and linear amplification or reduction of the BT trace relative to the corresponding grid. Six pieces of information are needed to obtain the constants $a, b, c, \ldots, f$ of the transform, such as the x, y coordinates of three corners of the grid appearing with the trace.

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NOTES

Relationship Between Shell-Weight and Age in Certain Molluscs

Growth of molluscs is usually measured as increase of linear dimensions. It is not generally appreciated that there are certain advantages to measuring growth in terms of weight (Haskin, 1954; McHugh et al., 1958), and it has not been used very much in fishery studies.

Weight measurements cannot be made easily at sea; but on land, either in the laboratory or in the field, they can be made rapidly and accurately. They have been used in studies of daily growth of oysters (Havinga, 1928; Andrews, 1961). The animals were weighed in water and it was possible to measure very small changes in the weights of the shells. Walne (1958) measured total weights (animal and shell) of oysters of known age and found that the annual weight increment was constant between the ages of $1\frac{1}{2}$ and 6 years.

I have found that in certain other molluscs the annual weight increment of the shell is constant for a considerable proportion of the life span, and the relationship between shell-weight and age is therefore linear.

Shells were cleaned and left for a few days to come to equilibrium with atmospheric humidity. They were then weighed. Determinations were also made of dry weight on some samples (dried at 110 C). The difference between these determinations and those made at normal atmospheric humidity were negligible.

Cardium edule.—Shell-growth in the cockle is seasonal and takes place in summer (Orton, 1926). When growth begins again each spring a mark is left on the shell and it is possible to determine the age of the shell by counting these "growth rings." Measurement of age by means of growth rings has to be carried out with care because under certain conditions more than one ring may be formed each year. The sample used for this study formed part of a population which has been thoroughly investigated by Hancock and Urquhart (1965), and it is certain that the ages given for the shells are correct. The relationship between shell-weight and age is clearly linear (Fig. 1), and although the dispersion of weight about the mean is relatively greater than that of length, the separation of older year-groups is greater in terms of weight.

Mercenaria mercenaria.—Shell-growth of the hard clam is also seasonal (Belding, 1912), and growth rings are formed. Age was determined by counting these rings and it was assumed that they were annual in all the specimens examined. Although very few old specimens were obtained, a linear relationship

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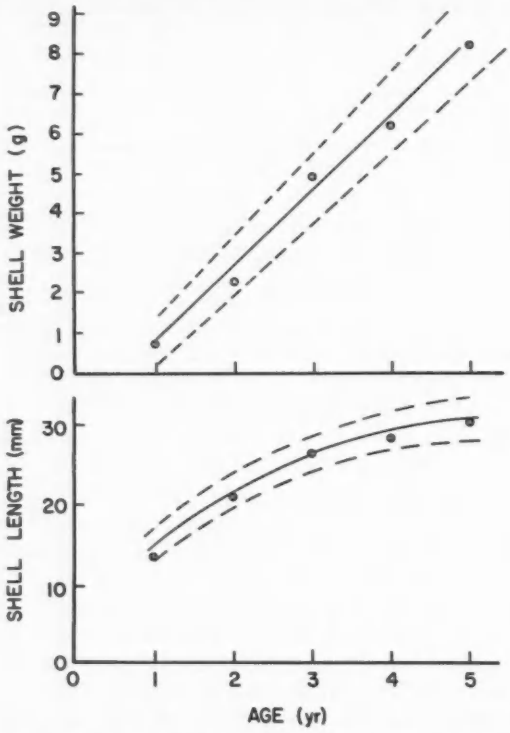

FIG. 1. Shell-weight and length of *Cardium edule* from the Llanrhidian Sands, Glamorganshire, Wales. Sample taken May 1963. The broken lines represent approximately 1 standard deviation from the mean. The mean curve (solid line) of the shell-weight graph was fitted by eye; that of the shell-length graph represents the function $L = 24t^{\frac{1}{3}}-9$, where L is shell-length in millimetres and t is age in years.

of shell weight to age appeared to exist between ages of 2 and 8 years (Fig. 2A). Haskin (1954) gave examples of total weight and age for *M. mercenaria*, and although he did not specifically discuss the relationship, it is approximately linear in many of his examples.

Crepidula fornicata.—There are no prominent growth features on many of the shells of this colonial gasteropod. Solitary individuals may show annual growth rings but the most prominent feature on those forming part of a chain is the scar caused by the foot and shell margin of the individual attached to the dorsal surface (Walne, 1956). However, this scar is confined to the periostracum and growth rings can be brought to light simply by leaving the shells exposed to the weather. The relatively gentle action of weathering removes the periostracum and slightly etches the shell, and growth rings can be seen easily.

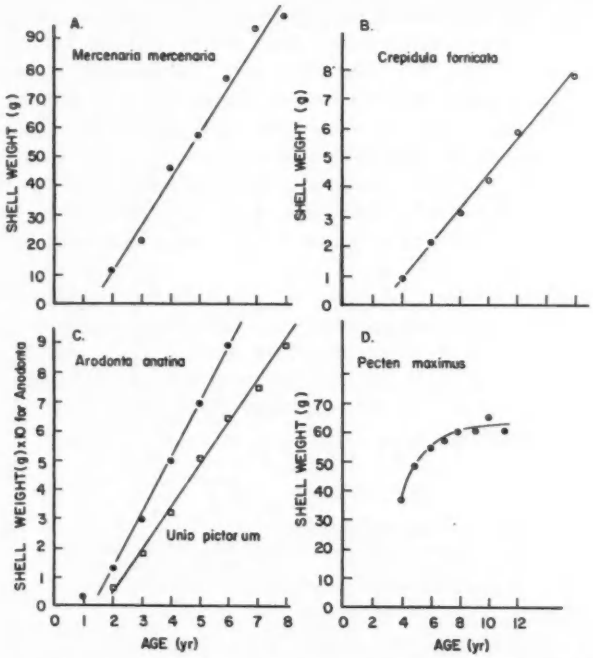

FIG. 2. Relationship between shell-weight and age. A, sample taken May 1964 from Southampton Water, Hampshire, England. B, sample taken July 1963 from the River Crouch, Essex, England. C, from the River Thames, England. Data from Negus (1966). D, sample taken October 1964 from the Isle of Man, Irish Sea. In A, B, and D the variation about the mean is similar in proportion to that of *Cardium edule* (Fig. 1).

This effect could not be produced by relatively rapid chemical removal of the periostracum.

If chains of *C. fornicata* were left above high-water mark the animals died within a few days and the flesh rapidly decayed. Single shells could then be spread thinly over the ground for maximum exposure to weathering. After about 4 weeks much of the periostracum had weathered away and growth rings could be seen on about 50% of the shells examined. After 12 weeks growth rings were visible on nearly all the shells.

There was no definite evidence that these rings were annual, but the shells were aged on the assumption that they were. The growth data obtained were in reasonable agreement with the results of Walne (1956). The oldest specimens examined were 8 years old and the shell-weight and age relationship was linear between ages of 2 and 8 years (Fig. 2B).

Anodonta anatia and *Unio pictorum*.—Negus (1966) measured shell-weight and age of three species of freshwater pelecypod. The relationships seem to be

curvilinear but this is because log shell-weight is used as ordinate. When shell-weight is put on an arithmetic scale the relationships become linear for two of these species (Fig. 2C). The other species measured by Negus (1966), *Unio tumidus*, has a shell-weight to age relationship which is curved.

Ostrea edulis.—It is difficult to determine the age of oyster shells. However, frequency distributions of shell-weight have modes spaced at equal intervals (Fig. 3) indicating that in this species also the shell-weight and age relationship could be approximately linear. The weight of the right (flat) valve was measured because the growth of this valve is less likely to be affected by environmental influences.

In Fig. 3A the modes at 13 g and 17 g probably represent groups of 4- and 5-year-old oysters. These modal sizes were plotted on Fig. 4, the curve was linearly extrapolated, and estimates of the modal weights of 3- and 6-year groups were made. The predicted positions of the 3- and 6-year groups on the frequency distribution are not unreasonable (Fig. 3A). There could be half-hidden modes at these points.

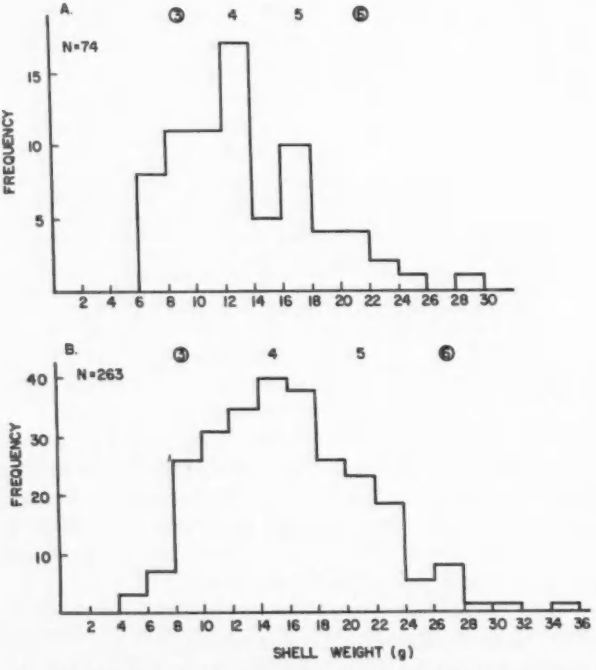

FIG. 3. Shell-weight frequency distributions of right valves of *Ostrea edulis*. A, sample taken April 1963 from the River Fal, Cornwall, England; B, sample taken April 1963 from the River Crouch, Essex, England. The numbers above the histograms refer to year-groups, those in circles are the year-groups predicted by extrapolations on Fig. 4.

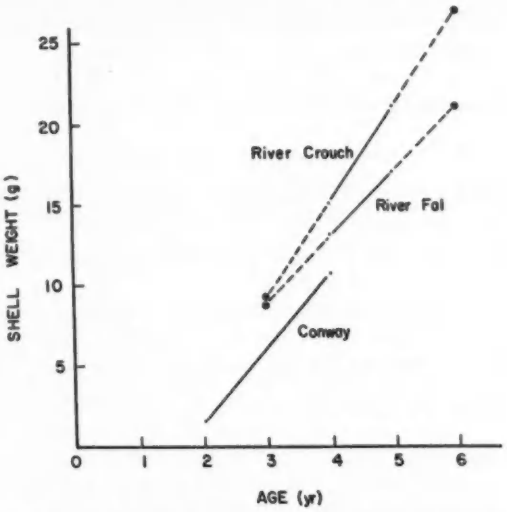

FIG. 4. Relationship between shell-weight (right valves) and age of *Ostrea edulis*. The ages of the samples from the River Fal and River Crouch were estimated from Fig. 3. The ages of the Conway sample were known.

Similarly, the modes at 15 g and 21 g in Fig. 3B probably represent 4- and 5-year groups. Plotting these values on Fig. 4 and extrapolating gives estimates of modal shell-weight for 3- and 6-year groups. These also fall at reasonable points on the frequency distribution (Fig. 3B).

The shell-weights of a small sample (less than 10 individuals of each age) of oysters of known age are also shown in Fig. 4, and compare favourably with the estimates from the samples of unknown age.

Pecten maximus.—In the scallop the shell-weight and age relationship was curvilinear (Fig. 2D) and was of similar form to that of linear dimensions and age. The example given is for right (flat) valves, but similar results were obtained for left valves. Age was estimated by counting growth rings and it was assumed that these were annual (Mason, 1957).

It has been definitely established that the relationship between size and age of animals follows a sigmoid curve. This can be expressed precisely in mathematical terms — for instance, Weymouth and McMillin (1930) showed that $L = Be^{-ce^{-kt}}$ described the growth of the razor clam, *Siliqua patula* (where L is length at time t and B, C, and k are constants) — but it cannot be easily manipulated for computational purposes. The growth of both mammals (Brody, 1945) and fish (Ricker, 1958) is sigmoid when expressed either in terms of linear dimensions or in terms of weight.

However, for certain molluscs which do not reach a maximum size (within the range of age and size commonly observed) the relationship between shell weight and age approximates to a linear function. The exact reasons for this

are probably complex, but explanations can be offered if certain simplifying assumptions are considered.

In Fig. 1 the curve for shell-length and age of *Cardium edule* is not the best curve which could be fitted to the points. It represents the simple cubic function

$$L = 24t^{\frac{1}{3}} - 9 \quad \ldots\ldots(1)$$

(where L is shell-length in millimetres and t is age in years), but it is a good approximation *over the range of size and age considered.* The relationship between shell-weight and length is also a simple cubic function, namely

$$L = 15W^{\frac{1}{3}} \quad \ldots\ldots(2)$$

(where L is shell-length in millimetres and W is weight in grams). There is no simple relationship between these two functions (the presence of the second constant in equation 1 introduces complications), but it is self evident that if L varies approximately as $t^{\frac{1}{3}}$ and also varies as $W^{\frac{1}{3}}$, then W will vary approximately as t.

One other factor might contribute to a linear shell-weight and age relationship. The annual increment of linear dimensions of old shells is small, but considerable shell thickening can occur. This could increase the slope of the proximal part of the growth curve (of weight) so that it would tend towards linearity.

For certain species with no reliable growth features on the shell and with a linear shell-weight and age relationship it is possible to use shell-weight as an approximate measure of age. The age structure of populations with a restricted breeding season can be determined by measuring shells and identifying year-groups from size-frequency distributions. If linear dimensions are used it is often not possible to separate older year-groups because the annual increment is small. However, the annual weight increment is constant, and year-groups of all ages are equally separated on frequency distributions of shell-weight.

The determination of age by means of shell-weight may have applications to fossil populations. In these, age structures are not often preserved. I have shown that information on growth can be obtained from frequency distributions for certain kinds of fossil population (Sheldon, 1965). By using shell-weight instead of linear dimensions, more effective analysis might be possible.

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Toxicities of Two Insecticides to Young Coho Salmon

Laboratory tests were carried out to determine the relative resistance of coho salmon (*Oncorhynchus kisutch*) to two insecticides: C-8514, a formamidin compound, and BHC. The BHC formulation employed is one of a type used to spray sawlogs against *Ambrosia* beetle infestation. The formamidin preparation was suggested as a possible alternative to BHC. The spraying of logs with insecticide poses a potential threat to young salmon in treated areas. Tests of the comparative toxicities of the two formulations were made on young coho salmon, a species usually indigenous to areas in British Columbia where such insecticides are utilized.

The candidate formamidin insecticide, C-8514, was supplied by Ciba Co. Ltd. The formulation contained 600 g/litre of active ingredient (grams a.i./litre). The BHC (hexachlorocyclohexane) preparation, designated BHC .84-E, was an emulsifiable formulation of Stauffer Chemical Co., containing 1.0 lb/Imp gal of the gamma isomer. For testing purposes both formulations were diluted with fresh water. Young coho salmon used in the tests were hatched and reared at the Biological Station, Nanaimo. Prior to the tests the fry were held in fresh water at 12–14 C. Test conditions and average sizes of fish used are listed as follows:

Insecticide	Time of tests	Length, *cm*	Weight, *g*	Average test temperature, *C*
C-8514	April–May 1966	3.46	0.326	10.1
BHC	June 1966	4.13	0.635	12.2

Experiments were conducted in a battery of 40-litre tanks. During each battery of tests, a stock solution of insecticide was delivered to the dosing apparatus from a reservoir. Contents of the reservoir were stirred and renewed every 24 hr to minimize possible problems arising from physical or chemical deterioration of the formulations. Constant flows of dilutions of the toxicants were dispersed to the tanks through apparatus modified from a design of Abram (1960). Flow rates of 500 ml/minute of toxicant at required dilution levels were maintained over the test periods for each of the several concentrations of the two insecticides.

Single samples of 10 fish were exposed to each of 12 concentration levels of C-8514 and to each of 11 concentration levels of BHC (Table I). Time to 50% mortality for each concentration was estimated from probit plots (Bliss, 1937) of the individual resistance times.

The formamidin formulation did not form a stable emulsion in the concentrations maintained in the stock solution reservoir (0.025 and 2.5 mg a.i./litre). Precipitation of crystals, presumably of the formamidin compound,

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TABLE I. Estimates of time to 50% mortality (ET50) for samples of 10 coho fry exposed to various concentrations of C-8514 and BHC in fresh water.

C-8514	ET50	BHC	ET50
mg a.i./litre	*min*	*mg a.i./litre*	*min*
1	>4,273	0.05	>7,160
5	>4,273	0.08	>20,167
7.5	>4,639	0.10	8,800
10	>4,639	0.12	8,630
15	6,400[a]	0.15	4,800[a]
17.5	5,900	0.20	4,825
20	1,010	0.25	2,000
30	745	0.30	704
35	524	0.50	500
40	105	0.75	625
50	13.5	1.00	550
100	7.4	1.00	720

[a]Approximation from truncated distribution.

occurred in the delivery lines to the test tanks. This problem was partially solved by purging of the delivery lines. Lack of stability of the formulation would suggest that the actual deliveries of insecticide to several of the low concentration (1, 5, 7.5 mg a.i./litre) tests were somewhat lower than indicated in the table.

Comparison of the resistance time-concentration relationships for the two insecticide preparations is illustrated in Fig. 1. The 48-hr median tolerance limits (48-hr TL_m) for the insecticides were estimated from the relationships as:

C-8514 — 21.5 mg a.i./litre;
BHC — 0.20 mg a.i./litre.

Rapid mortality occurred in C-8514 concentrations above 30 mg a.i./litre and in BHC concentrations above 0.30 mg a.i./litre (Table I, Fig. 1). These observations of acute effects, and a comparison of the 48-hr TL_m concentrations, indicate that equivalent acute effects are produced by the BHC preparation at a concentration approximately $\frac{1}{100}$ that of the C-8514 formulation.

The rate of decay of the gamma isomer of BHC is suspected to be appreciable. Werner and Waldichuk (1961) found the half-life of the gamma isomer to be about 2 days in seawater at approximately 21 C. The half-life in fresh water would be somewhat longer, likely in the vicinity of 7–8 days (Werner, personal communication).

As noted, the formamidin compound produced acute toxic effects only at much higher concentrations than the BHC preparation. However, physical instability of the formamidin formulation tested would suggest that residual

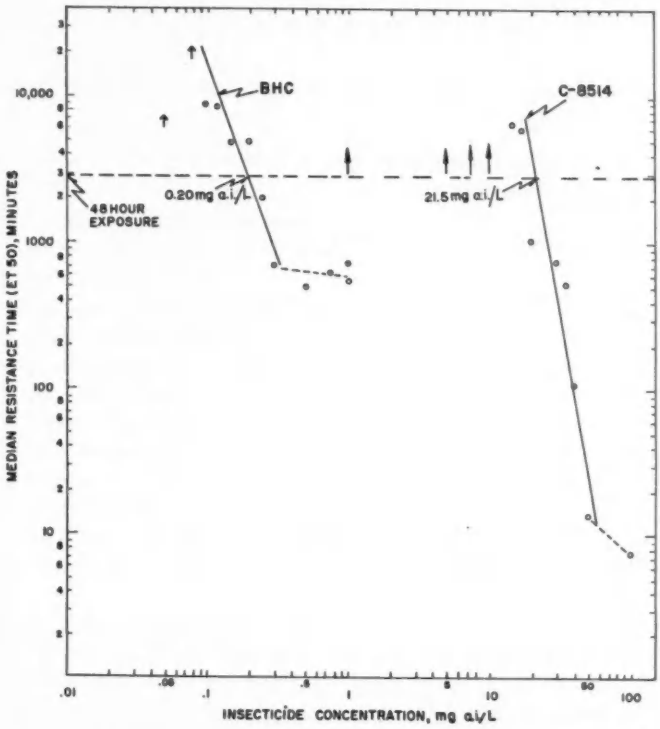

FIG. 1. Acute toxicities of C-8514 and BHC insecticides to juvenile coho salmon. The arrows signify the times of termination of tests in which all fish survived.

toxicity in the aquatic environment could be a problem were the preparation to be used on or near water courses under field conditions.

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The Gempylid *Nealotus tripes* New to the Canadian Atlantic

A specimen of the gempylid *Nealotus tripes* Johnson 1865 was taken on August 22, 1966, south of Sable Island Bank (43°30′40″N lat; 59°31′30″W long) (Fig. 1). It was captured alive at night (2101–2131 ADT) in a 1-m Neuston net towed alongside the research vessel C.G.S. *A.T. Cameron*. The surface water temperature was 17 C.

The specimen, which is stored (Cat. No. 24,996) at the Royal Ontario Museum, Toronto, Ontario, is 225 mm in fork length (210 mm standard length). The maximum body depth is 35.1 mm, the maximum body width is 21.7 mm, the head length is 56.7 mm and the horizontal width of the fleshy orbit is 11.5 mm. The fish was identified by Dr W. B. Scott of the Royal Ontario Museum and supports his earlier tentative assignation to this species of some gempylid remains found in the stomachs of swordfish taken from the area. Previous records of *Nealotus tripes*, as summarized by Grey (1953), are from Madeira (type specimen), the South Atlantic, the Gulf of Guinea, off Bermuda, and off Japan. Voss (1957) lists additional specimens from Bermuda.

Our specimen agrees with the type specimen in the number of dorsal spines (XXI) and pectoral rays (13). However, it differs from the type and agrees with the specimen of Matsubara and Iwai (1952) in having one less soft ray (18 + 2) and (17 + 2) in the dorsal and anal fins, and in having a second, very small spine posterior to the post-anal spine. The body is significantly stouter in both width and depth than in other specimens described.

Adult gempylids are generally considered to be deep-swimming fishes, with such records as there are for *N. tripes*, disregarding Günther's (1887) uncertain record, indicating a depth range of 914–1646 m (Voss, 1957). The present capture extends the known vertical range of *N. tripes* to the surface, at least at night, and the known geographical range approximately 650 miles to the northeast in the Northwest Atlantic Ocean.

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(FIG. 1 *opposite*)

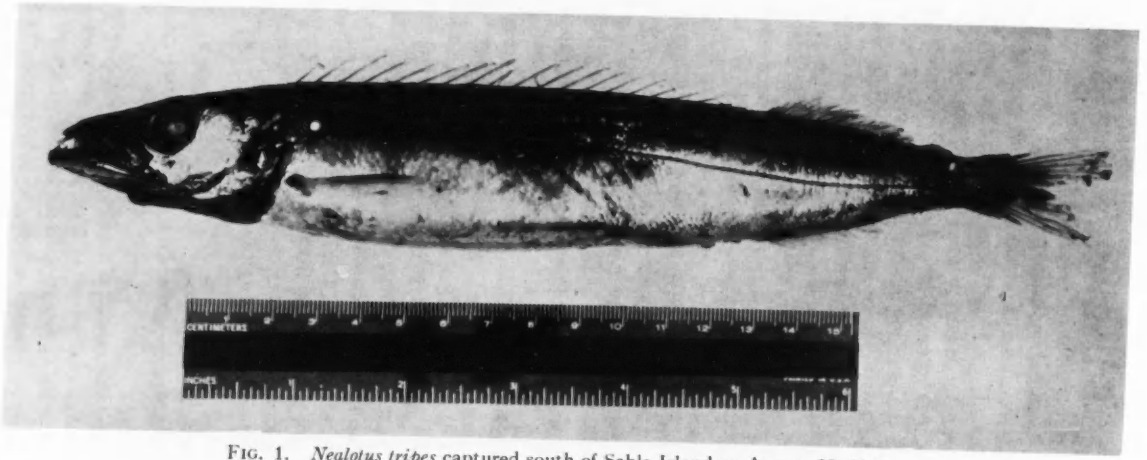

FIG. 1. *Nealotus tripes* captured south of Sable Island on August 22, 1966.

Bactericidal Effect of Acetylated Monoglycerides as Protective Coating on Frozen Fish

Recent developments in food technology in relation to the preservation of frozen foods have promoted the utilization of acetoglycerides (Feuge, 1955; Anon., 1955) and distilled acetylated monoglycerides (Feuge, 1960). When used as protective coating on frozen foods, these fatty substances are claimed to offer several interesting advantages as listed by Brokaw (1960).

Experiments on the use of edible acetylated monoglycerides as a protective coating have been described by Zabik and Dawson (1963) for cooked poultry and more recently by Ayres (1964) for frozen pork chops. This coating technique has appeared as one of the many possible applications for distilled acetylated monoglycerides which could upgrade consumer quality and increase storage life of frozen fish. In addition, it would seem to offer numerous advantages as a replacement for the laborious glazing process currently used for the storage of frozen fish in the round or the steak form.

The main concern of the present investigation is not to discuss the validity of the coating treatment to frozen fish or to evaluate its effect on storage life and keeping quality. Its purpose is to determine how the bacterial microflora originally present on the surface of the treated frozen fish is affected by the high heat of the coating procedure. This may have some significant bearing on the subsequent storage of the frozen fish, especially in retail stores where refrigeration facilities are inadequate or where storage temperatures are subjected to gross fluctuations.

The distilled acetylated monoglycerides used in the present studies are known under the trade name Myvacet Type 7-00, and have been kindly supplied by Distillation Products Industries, Division of Eastman Kodak Company, through their Canadian distributors, Tennant Smith Ltd.

All the experiments were conducted with fresh round cod frozen at −24 C (−11 F) and cut into sections of convenient size to be dipped into a container of boiling Myvacet. Bacterial populations were evaluated on surface skin samples and colonies were counted after incubation at 20 C for 5 days. This incubation time was sufficient to allow pinpoint colonies to become more distinguishable. Total counts were always reported on the basis of 100-cm^2 surface area.

Temperatures at the frozen fish surface were recorded by a Leeds and Northrup Speedomax potentiometer with a thermocouple giving readings at 4-sec intervals.

To obtain an idea of the effect of initial contamination on the bactericidal action of the high heat treatment to which the fish samples were subjected, fish in various stages of freshness were selected. This was done by allowing fresh cod to stand at room temperature for periods of time ranging from 6 to 30 hr. After freezing, samples of these fish were removed to obtain initial

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plate counts of surface contamination. The remaining portions were dipped in Myvacet at 160 C for 12 sec and refrozen. After 24 hr in cold storage, samples were again taken and total counts obtained for comparison. Table I lists the results obtained from several series of experiments. A selection has been made in order to cover a fairly wide range of initial contamination.

TABLE I. Effect of Myvacet coating on the surface microflora of frozen cod samples (bacteria counts/100 cm²).

Sample No.	Before treatment	After treatment	Per cent reduction
1	1.9×10^8	5.5×10^8	71
2	4.5×10^8	1.08×10^8	76
3	8.9×10^6	1.3×10^6	85
4	1.9×10^5	2.7×10^4	86
5	4.8×10^4	3.8×10^3	92

For all the samples, the observed inhibition caused by the Myvacet coating procedure ranged from 71 to 92%. As normally expected, inhibition was greater when initial contamination was more restricted. Just recently, Ayres (1964) has reported identical ranges of inhibition in his experiments on the hot-melt coating of frozen pork chops. Much of this destructive action resulted from the brief contact of the organisms at the surface with the hot liquid coating.

The reported data showed that an appreciable number of bacteria was not destroyed by the heat treatment and remained alive between the skin and protective coating. The reason for this survival was obtained by observing temperatures at or near the frozen surfaces where bacteria are located during the immersion period in the hot Myvacet. Thermocouples connected to the automatic recorder were placed at two different locations: one at the fish surface and the other just beneath the surface, under the scale layer. Readings were taken every 4 sec and the data obtained are illustrated in Fig. 1.

At the skin surface, where the bacterial contamination is concentrated, the highest temperature reached was 65 C after 12 sec. When the sample of frozen fish was removed from the Myvacet bath after 12 sec, the temperature dropped to 52 C in the next 4 sec. At the subsurface, where a more limited contamination is liable to take place due to bacterial penetration, bacteria were better protected against the heat treatment since the highest resulting temperature reached after 12 sec of immersion was 16.5 C, followed by a rapid drop to 5 C after removal from the hot bath.

The data show quite clearly that the resulting temperatures, after an immersion time of 12 sec, are relatively low and do not reach the levels necessary to insure a more complete destruction of the surface microflora, even if the latter is made up almost completely of heat-susceptible psychrophilic organisms. In processes where shorter immersion periods are recommended

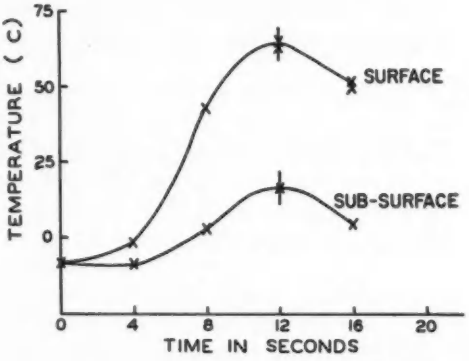

FIG. 1. Temperature changes at and near the frozen cod surface during immersion in Myvacet at 160 C (arrows indicate end of immersion).

(2 to 5 sec) the temperatures at the surface of the fish are much lower and the percentage reduction in total counts are expected to be proportionally decreased. It is well known that for an effective pasteurization of milk, the requirements are 30 min at 63 C by the ordinary process and 20 sec at 71 C by the flash process.

After coating and refreezing, the cod samples were incubated at defrost temperatures, 2 and 5 C. Core samples were taken for bacteriological analysis after 0, 3, 5, and 7 days of storage and total counts were determined. The results illustrated in Fig. 2 show that storage at the two defrost temperatures promoted the proliferation of the microflora remaining on the fish after the

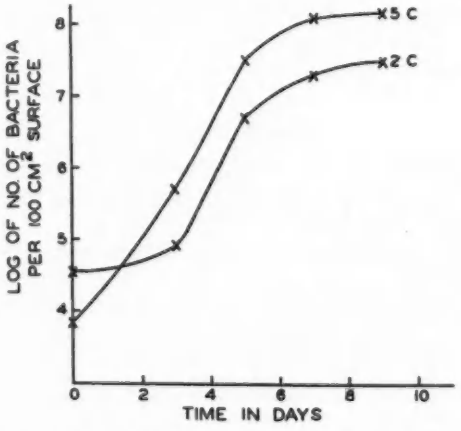

FIG. 2. Effect of defrost temperatures on the microflora of Myvacet treated cod samples.

coating treatment. After 7 days of storage the total numbers reached fairly high levels for the two temperatures, although a longer lag period was observed at 2 C.

Almost identical developments of psychrophilic bacteria have been observed in frozen chicken pie (Peterson and Gunderson, 1960) and in coated poultry (Meyer et al., 1959) stored at defrost temperatures. The latter workers have concluded that the two coating materials, agar and carrageenin gel, had limited value in retarding microbial spoilage of poultry stored at 2 C unless antibiotics of the tetracycline types were incorporated in the coating materials.

Following these observations, it seems that the effectiveness of acetylated monoglyceride coatings in the storage of frozen fish would be greatly enhanced by the addition of such antibiotics as chlortetracycline and oxytetracycline. However, in view of the heat lability of most antibiotics (Steiner and Tarr, 1956; Lerke and Farber, 1960; Tarr 1960), a dip treatment would have to be applied to the fish before freezing and coating. Thus, studies would have to be conducted for determining the proper concentration to be used in the dip solution so as to leave an effective and permitted residue after the coating treatment.

This combination of acetylated monoglyceride and antibiotic treatments may have an important significance to the frozen fish industry, since most of the organisms are confined to the surface and most spoilage problems are surface phenomena.

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